

Host relationships and geographic distribution of species of *Acanthobothrium* Blanchard, 1848 (Onchoproteocephalidea, Onchobothriidae) in elasmobranchs: a metadata analysis

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Abstract

Species of *Acanthobothrium* have been documented as parasites of the spiral intestine of elasmobranchs. Results of a metadata analysis indicate that 114 species of elasmobranchs have been reported as hosts of 200 species of *Acanthobothrium*. The metadata analysis revealed that 3.7% of species of sharks and 14.9% of species of rays that have been reported as hosts to date; some species are parasitized by more than one species of *Acanthobothrium*. This work provides a Category designation, as proposed by Ghoshroy and Caira (2001), for each species of *Acanthobothrium*. These Category designations are a tool to facilitate comparisons among members of *Acanthobothrium* for descriptions of new species in the future.

Keywords

Biodiversity, Elasmobranchii, Eucestoda, geographic distribution, rays, sharks

Introduction

According to Last et al. (2016b), there are 34 families comprised of 516 valid species of sharks and 26 families that include 633 valid species of rays. Since that publication, six new species of sharks and rays were described by: Yokota and Carvalho (2017) (two species of rays), Vaz and Carvalho (2018) (one species of shark), Rutledge (2019) (one species of ray), Grace et al. (2019) (one species of shark) and Concha et al. (2019) (one species of ray). This brought the current number of recognized species to 517 species of sharks and 637 species of rays.

Elasmobranchs (sharks, skates and rays) are host to a great variety of parasites in nature, particularly helminths. *Acanthobothrium* Blanchard, 1848 (Onchoproteocephalidea) is the most diverse genus that has been reported as parasite of the spiral intestine of elasmobranchs (Caira and Jensen 2017). At the present time, 201 species of *Acanthobothrium* are considered to be valid (Maleki et al. 2013; Caira and Jensen 2017; Rodríguez-Ibarra et al. 2018; Franzese and Ivanov 2018; Maleki et al. 2019; Zaragoza-Tapia et al. 2019, 2020). The genus consists of species that exclusively parasitize elasmobranchs as adults and, in many cases, individual species are thought to parasitize only a single species of elasmobranch (Caira 2011; Caira and Jensen 2017). Therefore, the genus *Acanthobothrium* is an excellent model for future studies of host-parasite co-speciation.

The main goal of this work is to provide a revised checklist based on a metadata analysis of the host relationships of members of *Acanthobothrium* and their geographic distribution based on records that have been generated from different parts of the world. The checklist focuses on the 201 valid species of *Acanthobothrium* and reports correlated with the genera and species of elasmobranchs, and includes the geographical distribution of each.

The number of species of Acanthobothrium continues to grow and there are still regions of the world without a single report of this genus (see Figure 1). For some time, the process of distinguishing new species of Acanthobothrium from existing species has become more and more unwieldy because of the large number of species. As an identification tool, Ghoshroy and Caira (2001) developed a categorical method for identifying species for initial comparisons. Therefore, in order to provide an update to this method, categorical designations are provided in the present checklist for each species of Acanthobothrium in the manner proposed by Ghoshroy and Caira (2001). The categories are based on and obtained from the combination of four quantitative characters: total length of the worm; the number of proglottids comprising the strobila; the number of testes per proglottid; and symmetry of the ovarian lobes. This categorical designation allows parasitologists working with this genus to postulate a group of similar species, those of the same category designation, for comparison of a new species or to aid in the preliminary identification of known species. As an additional aid, in the checklist the accession number, if known, of type specimens of each species is provided.

Materials and methods

The checklist, updated until March 2020, was based on bibliographical information from two sources of information: 1. a compilation of the records of species of *Acantho-bothrium* as originally described, complemented by information gathered from Global Cestode Database (Caira et al. 2019) and from recent compilation studies (e.g., Ghoshroy and Caira 2001; Campbell and Beveridge 2002; Fyler and Caira 2006; Caira and Jensen 2017); and 2. information for the distribution and taxonomy of elasmobranchs that integrated a bibliographical search using different databases of literature published to date (e.g., Del Moral-Flores et al. 2015; Last et al. 2016b; Merlo-Serna and García-Prieto 2016; Alves et al. 2017) and data from FishBase (Froese and Pauly 2019).

In the checklist, the species of *Acanthobothrium* are arranged in alphabetical order. The scientific names and geographic distribution of elasmobranchs have been updated based on Last et al. (2016a, 2016b), Amaral et al. (2018) and Froese and Pauly (2019). The regional classification scheme of the geographic distribution of the hosts is according to Last et al. (2016b) with additional information from Froese and Pauly (2019). The following abbreviations are used for biogeographic regions (see Figure 1):

ARC	Arctic Ocean;	NIO	Northern Indian Ocean;
ECA	Eastern Central Atlantic;	SOC	Southern (Antarctic) Ocean;
ECP	Eastern Central Pacific;	WCA	Western Central Atlantic;
EIO	Eastern Indian Ocean;	WCP	Western Central Pacific;
ENA	Eastern North Atlantic;	WIO	Western Indian Ocean;
ENP	Eastern North Pacific;	WNA	Western North Atlantic;
ESA	Eastern South Atlantic;	WNP	Western North Pacific;
ESP	Eastern South Pacific;	WSA	Western South Atlantic;
MED	Mediterranean Sea;	WSP	Western South Pacific.

Information for each species of *Acanthobothrium* presented herein includes the name of the species, authority (original description referenced in the literature cited), abbreviation of the name of the collection where specimens are deposited and the accession numbers of the specimens, followed by the status of the specimens (holotype, paratype, neotype, syntype or voucher). The acronym "NR" was used for data that are not reported in the original source. Localities (type or/and additional localities) were given and referenced in the literature cited. A Category designation was supplied for all species using the categorical method proposed by Ghoshroy and Caira (2001).

The categorical method was developed as a system of grouping species of *Acanthobothrium* based on the combination of four qualitative characters: the total length of worms- ≤ 15 mm = S (short) or > 15 mm = L (long); the number of proglottids comprising the strobila- ≤ 50 = F (few) or > 50 = M (many); the number of testes per proglottid- ≤ 80 = F (few) or > 80 = M (many); and symmetry of the ovarian lobes-symmetrical = S or asymmetrical = A. Of the possible combinations the following 10

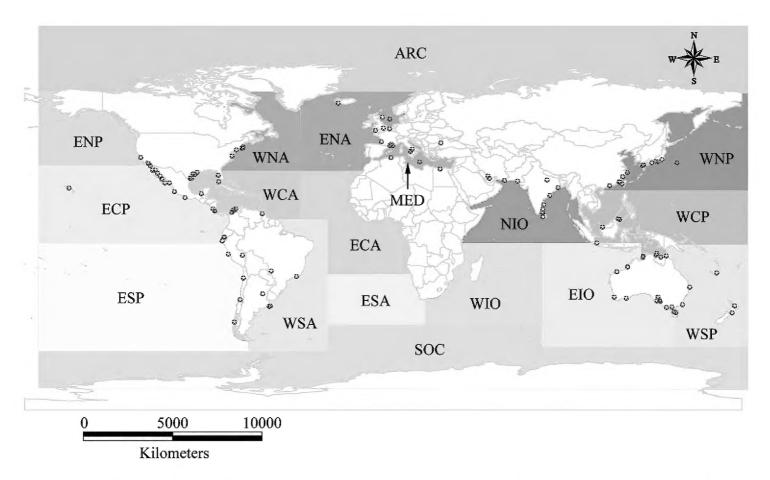


Figure 1. Type localities of species of *Acanthobothrium* reported worldwide and the biogeographic regions (Last et al. 2016b) of the geographic distribution of their hosts (see Table 1).

categories currently are recognized and coded as follows: 1 = SFFS; 2 = SFFA; 3 = LMMA; 4 = LMMS; 5 = LMFS; 6 = LMFA; 7 = LFFA; 8 = SMFS; 9 = LFFS; 10 = SMMS. This method limited the number of necessary comparisons required in the description between known species with new species assigned to the same Category. For this work, the categories and characteristics were used as in Ghoshroy and Caira (2001) and Fyler and Caira (2006) but the character values are as given in the original descriptions or as supplemented by the most recent taxonomic publications. In the Category designation, the type species is identified by number for this classification; the symbol "—" was used for the additional reports of species with additional hosts and/or localities. For specimens deposited in a formal collection, acronyms are as follows:

AMS Australian Museum, Sydney;

CH-MHNJP Colecciones Helmintológicas del Museo de Historia Natural "Javier

Prado" y del Instituto de Medicina Tropical "Daniel. A. Carrión", Uni-

versidad Mayor de San Marcos, Perú;

CHE Colección de Helmintos, Centro de Investigaciones Biológicas, Uni-

versidad Autónoma del Estado de Hidalgo, Pachuca, México;

CHIOC Coleção Helmintológica do Instituto Oswaldo Cruz, Rio de Janeiro,

Brazil;

CNHE Colección Nacional de Helmintos del Instituto de Biología, Universi-

dad Nacional Autónoma de México, México;

DMNZ Dominion Musem (=National Museum), New Zealand;DZAUW Department of Zoology, Andhra University, Waltair, India;

DZCJ Department of Zoology, Bipin Bihari, P. G. College, Jhansi, India;HWML University of Nebraska State Museum, Harold W. Manter Laboratory,

Division of Parasitology, Lincoln, Nebraska, United States;

IPCAS Institute of Parasitology, Academy of Sciences of the Czech Republic,

České Budějovice, Czech Republic;

IPMB Institut Penyelidikan Marin Borneo (Borneo Marine Research Insti-

tute), Universiti Malaysia Sabah, Kota Kinabalu, Sabah, Malaysia;

LRP Lawrence R. Penner Parasitology Collection, Helminthological Col-

lection, University of Connecticut, Storrs, Connecticut, United

States;

MACN-Pa Museo Argentino de Ciencias Naturales, Colección Parasitológica,

Buenos Aires, Argentina;

MEPN Museum of the Escuela Politecnica Nacional, Quito, Ecuador;

MHNLS Museo de Historia Natural La Salle, Caracas, Venezuela;

MHNP Museo de Historia Natural, Lima, Peru;

MLP Museo de Ciencias Naturales de La Plata, Departamento de Zoología

Invertebrados (Parasitología), Argentina;

MNHG Museum of Natural History, Geneva, Switzerland;

MNHN Muséum National d'Histoire Naturelle, Paris;MNHNC Museo Nacional de Historia Natural de Chile;MPM Meguro Parasitology Museum, Tokyo, Japan;

MZUM (P) Muzium Zoologi, Universiti Malaya, Kuala Lumpur, Malaysia;

MZUSP Museu de Zoologia da Universidade de São Paulo, Brazil;

NHMUK The Natural History Museum, London;

NMNS National Museum of Natural Science, Taichung, Taiwan;PRLXU Parasitology Research Laboratory, Xiamen University, China;

QM Queensland Museum, Brisbane, Queensland, Australia;

SAM AHC South Australian Museum, Adelaide, Australia;

SBC Sarawak Biodiversity Center, Kuching, Sarawak, Malaysia;

SPUK School of Parasitology, Department of Zoology, University of Karachi,

Pakistan;

SYSU School of Life Sciences, Sun Yat-sen University;

UAA Department of Zoology, University of Allahabad, Allahabad, India; USNPC United States National Parasite Collection, Beltsville, Maryland, Unit-

ed States;

ZCUOK Zoological Collection, University of Kurdistan, Sanandaj, Iran;

ZIMC Collection of the Zoological Survey of India, Indian Museum, Cal-

cutta and the Collection of the Department of Zoology, the University

of Allahabad, India;

ZMB Natural History Museum Berlin, Germany;

ZUTC Collection of the Zoological Museum, University of Tehran, Tehran, Iran.

designation obtained from Ghoshroy and Caira (2001); § = Category designation obtained from Fyler and Caira (2006); ¶ = Category designation obtained in this **Table 1.** Species of Acanthobothrium reported from the different species of elasmobranchs of the world. Abbreviations: Gd = Geographical distribution; Ht = Holotype; Nt = Neotype; Pt = Paratype; Va = Voucher; Loc = Locality; Sou = Source; Cd = Category designation; * = Additional host; † = Additional locality; ‡ = Category study from original descriptions; ** = Host identification requiring confirmation.

Species of Acanthobothrium	Ht	Nt, Pt or Va	Species of Host	рS	Loc	Sou	РЭ
A. adlardi Campbell & Beveridge, 2002	SAM AHC 28210	SAM AHC 22723, 22724	Pristiophorus cirratus (Latham, 1794)	EIO, WSP	Port Stanvac, South Australia	Campbell and Beveridge (2002)	48
A. aetiobatidis (Shipley, 1900) Southwell, 1925	NR	NR	Aetobatus narinari** (Euphrasen, 1790)	WSA, WCA, WNA, ECA	Lifu, Loyalty Islands	Shipley (1900), Southwell (1925), Baer and Euzet (1962), Goldstein (1967)	\$9
A. amazonensis Mayes, Brooks & Thorson, 1978	USNPC 74806	USNPC 74807; HWML 20562	Potamotrygon circularis German, 1913	WSA	Itacuari River, Brazil	Mayes et al. (1978)	5‡
A. americanum Campbell, 1969	USNPC 71355	USNPC 71356	Hypanus americanus (Hildebrand & Schroeder, 1928)	WSA, WCA, WNA	Chesapeake Bay, Virginia, USA	Campbell (1969)	‡ 9
A. americanum†	NR	NR	Hypanus americanus	WSA, WCA, WNA	Isla Margarita, Venezuela	Mayes and Brooks (1981)	I
A. angelae Campbell & Beveridge, 2002	SAM AHC 22661	SAM AHC 22709, 22712	Hypnos monopterygius (Shaw, 1795)	EIO, WSP	Yarraville Shoals, South Australia	Campbell and Beveridge (2002)	58
A. annapinkiensis Carvajal & Goldstein, 1971	MNHNC 20.003	NR	Zearaja chilensis (Guichenot, 1848)	ESP, WSA,	Anna Pink Bay, Chile	Carvajal-G. and Goldstein (1971)	2‡
A. arlenae Campbell & Beveridge, 2002	SAM AHC 28225	SAM AHC 28226	Aetobatus narinari**	WSA, WCA, WNA, ECA	Fog Bay, Timor Sea, North Australia	Campbell and Beveridge (2002)	\$9
A. asnihae Fyler & Caira, 2006	MZUM (P) 142	USNPC 96413; LRP 3809-3812, LRP 3814 (including cross sections and SEM specimens); MZUM (P) 143–144; IPMB 77.14.04	Urogymnus polylepis (Bleeker, 1852)	NIO, WCP	Off Kampung Abai, Kinabatangan River, Sabah, Malaysia	Fyler and Caira (2006)	18
A. asrinae Maleki, Malek & Palm, 2015	ZUTC 1325	ZUTC 1326; ZMB E.7569; SEM voucher ZUTC 1327	Rhynchobatus cf. djiddensis** (Forsskå, 1775)	WIO, NIO	Persian Gulf, Iran	Maleki et al. (2015)	19

Cd	a) 1‡	38	lge –	73) 4‡	73) –	lge 1§	7(2)‡	ا. - G.	-G.	-	29
Sou	Marques et al. (1997a)	Robinson (1965)	Campbell and Beveridge (2002)	Appy and Dailey (1973)	Appy and Dailey (1973)	Campbell and Beveridge (2002)	Euzet (1955)	Carvajal-G. and Jeges-G. (1980)	Carvajal-G. and Jeges-G. (1980)	Escalante-A. (1986)	Lönnberg (1889)
Loc	Puerto Bolivar, Provincia de El Oro, Ecuador	Eden, New South Wales, Australia	Beachport, South Australia	San Quintin Bay, Baja California, Mexico	Newport Bay, California, USA	Broome, Western Australia	Mediterranean Sea, Gulfe du Lion	Antofagasta, Chile	Coquimbo, Chile	Trujillo, Peru	Mediterranean Sea
PЭ	ECP, ESP	ENA, MED, ECA, ESA, WIO, EIO, WSP	ENA, MED, ECA, ESA, WIO, EIO, WSP	ECP, ESP	ECP, ESP	WIO, NIO	ENA, MED, ECA, ESA, WIO	ESP	ESP	ESP	ENA, MED, ECA, ESA, WIO
Species of Host	<i>Gymnura afuerae</i> (Hildebrand, 1946)	Squalus megalops (Macleay, 1881)	Squalus megalops	Heterodontus francisci (Girard, 1855)	Heterodontus francisci	Rhynchobatus djiddensis**	<i>Myliobatis aquila</i> (Linnaeus, 1758)	<i>Myliobatis chilensis**</i> Philippi, 1892	Myliobatis chilensis**	Myliobatis chilensis**	<i>Raja clavata</i> Linnaeus, 1758
Nt, Pt or Va	MNHG 22098; CNHE 3029	AMS	SAM AHC 22696	USNPC 72568	NR	NR	NR	MNHNC 20015	NR	NR	NR
Ht	MEPN 3029	AMS	NR	USNPC 72567	NR	SAM AHC 28235	NR	NR	NR	NR	NR
Species of Acanthobothrium	A. atahualpai Marques, Brooks & Barringa, 1997	A. australis Robinson, 1965	A. australis†	A. bajaensis Appy & Dailey, 1973	A. bajaensis†	A. bartonae Campbell & Beveridge, 2002	A. batailloni Euzet, 1955	A. batailloni*†	A. batailloni*†	A. batailloni*†	A. benedenii (Lönnberg, 1889)

Species of Acanthobothrium	Ht	Nt, Pt or Va	Species of Host	РЭ	Loc	Sou	Cd
A. benedenii*†	NR	NR	Pteroplatytrygon violacea** (Bonaparte, 1832)	ENP, ECP, ESP, WSA, WCA, WNA, ENA, MED, ECA, ESA, WIO, NIO, EIO, WSP, WCP, WNP	Naples, Italy	Baer (1948)	1
A. benedenii*† 	NR	NR	<i>Torpedo marmorata**</i> Risso, 1810	ENA, MED, ECA, ESA	Casablanca, Marruecos	Euzet (1952), Euzet (1959)	I
A. bengalense Baer & Euzet, 1962	NR	NR	Pastinachus sephen (Forsskål, 1775)	NIO	Nagapattinam, India	Baer and Euzet (1962)	48
A. blairi Campbell & Beveridge, 2002	SAM AHC 28211	SAM AHC 28212	Dipturus whitleyi (Iredale, 1938)	EIO, WSP	Stanley, Tasmania	Campbell and Beveridge (2002)	38
A. blairi†	NR	NR	Dipturus whitleyi	EIO, WSP	Spencer Gulf, South Australia	Campbell and Beveridge (2002)	1
A. bobconniorum Fyler & Caira, 2010	QM G232499	QM G232500– G232501; USNPC 104278; LRP 7583–7585; cross sections of one paratype worm and voucher LRP 7586, 7588, 7589, SEM LRP 7587–7590	Rhynchobatus laevis** (Bloch & Schneider, 1801)	NIO, WNP	Gove Harbor, Gulf of Carpentaria, Northern Territory, Australia	Fyler and Caira (2010)	5 0
A. brachyacanthum Riser, 1955	USNPC 37418	NR	Raja stellulata (Gilbert, 1915)	ENP, ECP	Monterey Bay, California, USA	Riser (1955)	2‡
A. brachyacanthum*	NR	NR	Beringraja binoculata** (Gilbert, 1855)	ENP, ECP	Monterey Bay, California, USA	Riser (1955)	I
A. brayi Campbell & Beveridge, 2002	SAM AHC 22670	SAM AHC 22730	Sutorectus tentaculatus (Peters, 1864)	EIO, WSP	Eastern Shoal, South Australia	Campbell and Beveridge (2002)	28
A. brevissime Linton, 1909	USNPC 9008	NR	Hypanus say (Lesueur, 1817)	WSA, WCA, WNA	Dry Tortugas, Florida, USA	Linton (1908), Goldstein (1964)	24

Species of Acanthobothrium	Ht	Nt, Pt or Va	Species of Host	PS	Loc	Sou	СД
A. brevissime*†	NR	NR	Raja eglanteria Bosc, 1800	WCA, WNA	Gulf of Mexico, Chesapeake Bay, Virginia, USA	Campbell (1969)	1
A. brevissime*†	NR	USNPC 71349, 71350	Hypanus americanus	WSA, WCA, WNA	Gulf of Mexico, Chesapeake Bay, Virginia, USA	Campbell (1969)	ı
A. brevissime*†	NR	CH-MHNJP 727	Myliobatis peruvianus** Garman, 1913	ESP	Lima, Peru	Tantaleán-Vidaurre (1991)	ı
A. brevissime†	USNPC 9008	USNPC 60178 (neotype)	Hypanus say	WSA, WCA, WNA	Gulf of Mexico, Chesapeake Bay, Virginia, USA	Campbell (1969), Vardo- Zalik and Campbell (2011)	I
A. bullardi Ghoshroy & Caira, 2001	CNHE 4045	CNHE 4046–4047; LRP 2060–2062; USNPC 90466– 90468	Hypanus dipterurus (Jordan & Gilbert, 1880)	ECP	Bahía de Los Angeles, Gulf of California, Mexico	Ghoshroy and Caira (2001)	2#
A. bullardi‡	NR	NR	Hypanus dipterurus	ECP	Puertecitos, Gulf of California, Mexico	Ghoshroy and Caira (2001)	ı
A. bullardi†	NR	NR	Hypanus dipterurus	ECP	Santa Rosalia, Gulf of California, Mexico	Ghoshroy and Caira (2001)	I
A. cairae Vardo-Zalik & Campbell, 2011	USNPC 103801	USNPC 103802– 103814	Bathytoshia centroura (Mitchill, 1815)	WSA, WCA, WNA	Narragansett Bay off Sakonnet Point, Rhode Island, USA	Vardo-Zalik and Campbell (2011)	34
A. campbelli Marques, Brooks & Monks, 1995	MNHG 20014	MNHG 20015– 20016; HWML 38546; CNHE 3033	Urotrygon chilensis (Günther, 1872)	ECP, ESP	Costa de Pajaros, Puntarenas, Costa Rica	Marques et al. (1995)	2‡
A. campbelli*†	NR	MEPN 3033	Hypanus longus (Garman, 1880)	ECP	Puerto Huatulco, Provincia de El Oro, Ecuador	Marques et al. (1997a)	I
A. cannoni Campbell & Beveridge, 2002	SAM AHC 28236	SAM AHC 28237	Himantura uarnak (Gmelin, 1789)	WIO, NIO, EIO, WCP	Fog Bay, Timor Sea, North Australia	Campbell and Beveridge (2002)	48
A. cartagenensis Brooks & Mayes, 1980	USNPC 75159	NR	Urobatis jamaicensis (Cuvier, 1816)	WCA, WNA	Cartagena, Colombia	Brooks and Mayes (1980)	16

Species of Acanthobothrium	Ht	Nt, Pt or Va	Species of Host	РS	Loc	Sou	СД
A. cartagenensis†	NR	CNHE 9706; HWML 101020; CHE P00061	Urobatis jamaicensis	WCA, WNA	Ría Lagartos, Yucatán, Quintana Roo	Monks et al. (2015)	1
A. cartagenensis†	NR	CNHE 9706; HWML 101020; CHE P00061	Urobatis jamaicensis	WCA, WNA	Isla Contoy, Quintana Roo	Monks et al. (2015)	I
A. cartagenensis†	NR	CNHE 9706; HWML 101020; CHE P00061	Urobatis jamaicensis	WCA, WNA	Isla Cozumel, El Paso de los Cedros, Quintana Roo	Monks et al. (2015)	I
A. cartagenensis†	NR	CNHE 9706; HWML 101020; CHE P00061	Urobatis jamaicensis	WCA, WNA	Xcalak, Quintana Roo	Monks et al. (2015)	I
A. cestraciontis (Yamaguti, 1934)	NR	NR	Heterodontus japonicus Miklouho-Maclay & Macleay, 1884	WNP, WCP	Pacific Ocean, Japan	Yamaguti (1934)	4§
A. cestraciontis†	NR	NR	Sphyraena japonica** (Bloch &Schneider, 1801)	۸.	Pacific Ocean, Japan	Goldstein (1967)	I
A. chabahariense Maleki, Malek & Rastgoo, 2018	ZCUOK 100	ZCUOK 101–112 and (SME specimen) ZCUOK 113	Pastinachus cf. sephen**	OIN	Chabahar coasts, the coast of the Gulf of Oman, Iran	Maleki et al. (2018)	16
A. chengi Cornford, 1974	USNPC 72958	USNPC 72959	Bathytoshia lata (Garman, 1880)	ECP, ENA, MED, ECA, WIO, NIO, EIO, WSP, WCP, WNP	Oahu, Hawaii	Cornford (1974)	38
A. chilensis Rego, Vincente & Herrera, 1968	CHIOC 30.308 a-c	NR	Sarda chiliensis** (Cuvier, 1832)	۸.	Paita, Piúra, Peru	Rêgo et al. (1968)	÷÷.
A. chisholmae Campbell & Beveridge, 2002	SAM AHC 28223	SAM AHC 28224	Pastinachus sephen**	OIN	Nickol Bay, Western Australia	Campbell and Beveridge (2002)	28
A. cimari Marques, Brooks & Monks, 1995	MNHG 20017	MNHG 20018– 20020; HWML 38547	Hypanus longus	ECP	Punta Morales, Puntarenas Province, Costa Rica	Marques et al. (1995)	2‡
A. clarkeae Campbell & Beveridge, 2002	SAM AHC 28349	SAM AHC 28350	Urolophus paucimaculatus Dixon, 1969	EIO, WSP	Queenscliff, Victoria, Australia	Campbell and Beveridge (2002)	18

Species of Acanthobothrium	Ht	Nt, Pt or Va	Species of Host	PS	Loc	Sou	РЭ
A. clarkeae*†	NR	SAM AHC 28243, 28244	Urolophus cruciatus (Lacepède, 1804)	EIO, WSP	Devonport, Tasmania	Campbell and Beveridge (2002)	I
A. clarkeae*†	NR	SAM AHC 28208	Urolophus expansus McCulloch, 1916	EIO	Beachport, South Australia	Campbell and Beveridge (2002)	I
A. cleofanus Monks, Brooks & Lonce de Leon, 1996	CNHE 2670	CNHE 2671; MNHG 38576; HWML 38576.	Hypanus longus	ECP	Chamela Bay, Jalisco, Mexico	(Monks et al. 1996)	÷÷
A. colombianum Brooks & Mayes, 1980	USNPC 75160	USNPC 75161	Aetobatus narinari	WSA, WCA, WNA, ECA	Cartagena, Colombia	Brooks and Mayes (1980)	+6
A. confusum Baer & Euzet, 1962	NR	NR	Neotrygon kuhlii** (Müller & Henle, 1841)	WSP	Indian Ocean, Sri Lanka	Baer and Euzet (1962)	58
A. coquimbensis Carvajal & Jeges, 1980	MNHNC 20016	NR	Myliobatis chilensis	ESP	Antofagasta, Chile	Carvajal-G. and Jeges-G. (1980)	2‡
A. coquimbensis†	NR	NR	Myliobatis chilensis	ESP	Coquimbo, Chile	Carvajal-G. and Jeges-G. (1980)	I
A. coronatum (Rudolphi, 1819), Blanchard, 1848	NR	NR	Dipturus batis (Linnaeus, 1758)	ENA	Mediterranean Sea, Italy	Rudolphi (1819), Baer (1948)	48
A. coronatum*	NR	NR	Scyliorhinus stellaris (Linnaeus, 1758)	ENA, MED, ECA	Mediterranean Sea, Italy	Rudolphi (1819), Baer (1948)	I
A. coronatum*	NR	NR	Torpedo marmorata	ENA, MED, ECA, ESA	Mediterranean Sea, Italy	Rudolphi (1819), Baer (1948)	1
A. coronatum*	NR	NR	Torpedo torpedo (Linnaeus, 1758)	ENA, MED, ECA	Mediterranean Sea, Italy	Rudolphi (1819), Baer (1948)	ı
A. coronatum*	N.	NR	Dasyatis pastinaca (Linnaeus, 1758)	ENA, MED, ECA	Mediterranean Sea, Italy	Rudolphi (1819), Baer (1948)	I
A. coronatum*†	NR	NR	Hemitrygon akajei** (Müller & Henle, 1841)	WNP	Nakatsu, West Japan	Yoshida (1917)	I
A. coronatum*†	NR	NR	Aetobatus narinari**	WSA, WCA, WNA, ECA	Batavia, Java, Indonesia	MacCallum (1921)	ı
A. coronatum*†	NR	NR	Scyliorhinus stellaris	ENA, MED, ECA	Sète, France	Euzet (1959)	ı
A. coronatum $*$ †	NR	NR	Scyliorhinus stellaris	ENA, MED, ECA	Concarneau, France	Euzet (1959)	I
A. coronatum*†	NR	NR	Mustelus mustelus (Linnaeus, 1758)	ENA, MED, ECA, ESA	Naples, Italy	Euzet (1959)	ı

Species of Acanthobothrium	Ht	Nt, Pt or Va	Species of Host	РS	Loc	Sou	Cd
A. coronatum*†	NR	NR	Scyliorhinus stellaris	ENA, MED, ECA	Cardigan Bay, UK	Rees and Williams (1965)	l
A. coronatum*	NR	NR	Carcharodon carcharias (Linnaeus, 1758)	MED	Mediterranean Sea	Goldstein (1967)	I
A. coronatum*†	NR	MNHG 40003, 40009	Scyliorhinus canicula (Linnaeus, 1758)	ENA, MED, ECA	Naples, Italy	Euzet (1959), Vardo- Zalik and Campbell (2011)	1
A. costarricense Marques, Brooks & Monks, 1995	MNHG 20008	MNHG 20009– 20010; HWML 38544; CNHE 3034	Hypanus longus	ECP	Punta Morales, Puntarenas Province, Costa Rica	Marques et al. (1995)	2+
A. costarricense†	NR	MEPN 3034	Hypanus longus	ECP	Puerto Huatulco, Provincia de El Oro, Ecuador	Marques et al. (1997a)	I
A. crassicolle Wedl, 1855	NR	MNHG 40014 88/77	Dasyatis pastinaca	ENA, MED, ECA	Arcacho, Gironde, France	Dollfus (1926), Baer (1948), Goldstein (1967)	38
A. cribbi Campbell & Beveridge, 2002	SAM AHC 28251	SAM AHC 28252	Gymnura australis (Ramsay & Ogilby, 1886)	EIO, WSP, WCP	Gulf of Carpentaria, Northern Territory, Australia	Campbell and Beveridge (2002)	48
A. dasi Ghoshroy & Caira, 2001	CNHE 4043	CNHE 4044; HWML 15549– 15551; LRP 2051–2054; USNPC 90463–90465	Hypanus dipterurus	ECP	Puertecitos, Gulf of California, Mexico	Ghoshroy and Caira (2001)	2#
A. dasybati Yamaguti, 1934	NR	NR	Hemitrygon akajei	WNP	Tarumi, Kobe, Japan	Yamaguti (1934)	48
A. dasybati*†	NR	NR	Okamejei kenojei** (Müller & Henle, 1841)	WNP	Maisaka, Japan	Yamaguti (1952)	ı
A. dasybati*†	NR	NR	Urolophus $\operatorname{sp.}^{**}(U.$ fuscus?)	۸.	Hamazima, Mie, Japan	Yamaguti (1952)	I
A. dighaensis Srivastava & Capoor, 1980	UAA	NR	Pateobatis uarnacoides (Bleeker, 1852)	NIO, WCP	Digha, Orissa, India	Srivastav and Capoor (1980)	48
A. dollyae Caira & Burge, 2001	CNHE 4169	CNHE 4170; LRP 2097–2101; USNPC 90837–90839	Diplobatis ommata (Jordan and Gilbert, 1890)	ECP	Bahía de Los Angeles, Gulf of California, Mexico	Caira and Burge (2001)	15

Species of Acanthobothrium	Ht	Nt, Pt or Va	Species of Host	РЭ	Loc	Sou	Cd
A. dollyae†	NR	NR	Diplobatis ommata	ECP	Isla San Esteban, Gulf of California, Mexico	Caira and Burge (2001)	I
A. dollyae†	NR	NR	Diplobatis ommata	ECP	Punta Arena, Gulf of California, Mexico	Caira and Burge (2001)	1
A. dujardini van Beneden, 1850	NR	NR	Raja clavata	ENA, MED, ECA, ESA, WIO	English Channel, Belgium	van Beneden (1850), Goldstein (1967)	28
A. dujardini	NR	NR	Raja clavata	ENA, MED, ECA, ESA, WIO	English Channel, Belgium	Williams (1969)	I
A. dujardini*†	NR	NR	Raja brachyura** Lafont, 1871	ENA, MED, ECA	Roscoff, France	Euzet (1959)	I
A. dujardini*†	NR	NR	Raja montagui** Fowler, 1910	ENA, MED	British Isles	Williams (1960)	I
A. dysbiotos (MacCallum, 1921) Williams, 1969	NR	NR	Aetobatus narinari**	WSA, WCA, WNA, ECA	Batavia, Java, Indonesia	MacCallum (1921), Williams (1969)	48
A. edmondsi Campbell & Beveridge, 2002	SAM AHC 28205	SAM AHC 28206, 22704	Parascyllium ferrugineum McCulloch, 1911	EIO, WSP	Port Stanvac, South Australia	Campbell and Beveridge (2002)	58
A. edmondsi†	NR	NR	Parascyllium ferrugineum	EIO, WSP	Holdfast Bay, South Australia	Campbell and Beveridge (2002)	I
A. edmondsi†	NR	NR	Parascyllium ferrugineum	EIO, WSP	Esperance, Western Australia	Campbell and Beveridge (2002)	I
A. edwardsi Williams, 1969	NR	NR	Leucoraja fullonica (Linnaeus, 1758)	ENA, MED, ARC	West coast of Britain, United Kingdom	Williams (1969)	28
A. electricolum Brooks & Mayes, 1978	USNPC 74728	USNPC 74729	Narcine brasiliensis (Olfers, 1831)	WSA	Caribbean Sea, near Cartagena, Colombia	Brooks and Mayes (1978)	‡6
A. elongatum Subhapradha, 1955	NR	NR	Rhynchobatus djiddensis	WIO, NIO	Madras Coast, India	Subhapradha (1955)	49

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РЭ	88	1(8)	1	8(10)‡	1		<u>++</u>	I		5(8)‡
noS	Fyler and Caira (2006)	Zschokke (1888), Yamaguti (1959b)	Williams (1969)	Goldstein (1964)	Vardo-Zalik and Campbell (2011)	Campbell (1969)	Goldstein (1964)	Mayes and Brooks (1981)	Reyda and Caira (2006)	Marques et al. (1997b)
Loc	Off Kampung Abai, Kinabatangan River, Sabah, Malaysia	Mediterranean Sea	Mediterranean Sea	Gulf of Mexico and Coast of Massachusetts	Gulf of Mexico	Gulf of Mexico, Chesapeake Bay, Virginia, USA, USA	Northeastern Gulf of Mexico, Florida	Isla Margarita, Venezuela	Off Kampung Tetabuan, Sabah, Malaysia	Cuajiniquil Beach, Gulf of Santa Helena, Guanacaste, Costa Rica
РS	NIO, WCP	ENA, MED, ECA, ESA	ENA, MED, ECA	WCA, WNA	WCA	WCA, WNA	WSA, WCA, WNA, ECA	WSA, WCA, WNA, ECA	NIO, WCP	ECP
Species of Host	Urogymnus polylepis	Torpedo marmorata	Torpedo torpedo	Raja eglanteria	Raja texana Chandler, 1921	Raja eglanteria	Gymnura micrura (Bloch & Schneider, 1801)	Gymnura micrura	Pateobatis uarnacoides	Narcine entemedor Jordan & Starks, 1895
Nt, Pt or Va	USNPC 96414– 96415; LRP 3815- 3824 (including cross sections and SEM specimens); MZUM (P) 146; IPMB 77.14.05	NR	NR	NR	USNPC 103848- 103850	NR	NR	NR	USNPC 97463– 97464; LRP 3850– 3853 (including cross sections and SEM specimens); MZUM (P) 169(p)–171(p); IPMB 77.08.14	USNPC 87374; CHIOC 33754a, b; CNHE 3140
iΗ	MZUM (P) 145	NR	NR	USNPC 60025	NR	NR	USNPC 60024	NR	MZUM (P) 168(h)	CNHE 3139
Species of Acanthobothrium	A. etini Fyler & Caira, 2006	A. filicolle (Zschokke, 1888) Yamaguti, 1959	A. filicolle*	A. floridensis Goldstein, 1964	A. floridensis*†	A. floridensis†	A. fogeli Goldstein, 1964	A. fogeli†	A. foulki Reyda & Caira, 2006	A. franus Marques, Centritto & Stewart, 1997

Cq	19	38	38	58	28	15	\$(6)\$	5(9)2	38	48	ı	29
Sou	Maleki et al. (2015)	Campbell and Beveridge (2002)	Campbell and Beveridge (2002)	Sanaka et al. (1993)	Campbell and Beveridge (2002)	Reyda and Caira (2006)	Appy and Dailey (1973)	Severino and Sarmiento (1979)	Yamaguti (1952)	Yamaguti (1952), Yang et al. (2016)	Yamaguti (1952)	Yang et al. (2016)
Loc	Gulf of Oman, Iran	Nickol Bay, Western Australia	Fog Bay, Timor Sea, North Australia	Waltair coast, India	Goolwa, South Australia	Off Kampung Tetabuan, Sabah, Malaysia	Seal Beach, California, USA	Callao, Lima, Peru	Tokushima, Japan	East China Sea, Japan	East China Sea, Japan	Off Guanghai Port, Taishan, Guangdong Province, China
PS	WIO, NIO	OIN	WIO, NIO	WSA, WCA, WNA, ECA	MSP	NIO, WCP	ENP, ECP	ESP	WNP	WCP, WNP	WNP	WNP
Species of Host	Rhynchobatus cf. djiddensis**	Pastinachus sephen**	Rhynchobatus djiddensis**	Gymnura micrura**	Trygonorrbina fasciata Müller & Henle, 1841	Pateobatis uarnacoides	Platyrhinoidis triseriata (Jordan & Gilbert, 1880)	Myliobatis peruvianus	Narke japonica (Temminck & Schlegel, 1850)	Telatrygon zugei (Müller & Henle, 1841)	Hemitrygon akajei	Hemitrygon akajei
Nt, Pt or Va	ZUTC 1320–1323; ZMB E.7568; SEM voucher ZUTC 1324	SAM AHC 28218	NR	NR	SAM AHC 22715	USNPC 97465– 97466; LRP 3854– 3859 (includes cross sections and SEM specimens); MZUM (P) 173(p)–175(p); IPMB 77.08.15	USNPC 72570	CH-MHNJP 341, 341a, 341b	NR	NR	NR	MPM 21230; SYSU 20140818-1-4
Ht	ZUTC 1319	SAM AHC 28217	SAM AHC 28239	NR	SAM AHC 22600	MZUM (P) 172(h)	USNPC 72569	CH-MHNJP 340	NR	MPM 22638	NR	MPM 21229
Species of Acanthobothrium	A. fylerae Maleki, Malek & Palm, 2015	A. gasseri Campbell & Beveridge, 2002	A. gibsoni Campbell & Beveridge, 2002	A. giganticum Sanaka, Lakshmi & Hanumantharao, 1993	A. gloveri Campbell & Beveridge, 2002	A. gnomus Reyda & Caira, 2006	A. goldsteini Appy & Dailey, 1973	A. gonzalesmugaburoi Severino & Sarmiento, 1979	A. gracile Yamaguti, 1952	A. grandiceps Yamaguti, 1952	A. grandiceps*	A. guanghaiense Yang, Sun, Zhi, Iwaki, Reyda & Yang, 2016

Species of Acanthobothrium	Ht	Nt, Pt or Va	Species of Host	PS	Loc	Sou	Cd
A. hypermekkolpos Fyler & Caira, 2010	QM G232506	QM G232507; USNPC 104280; LRP 7591, hologenophores LRP 7592–7593	Rhynchobatus laevis**	NIO, WNP	Gove Harbor, Gulf of Carpentaria, Northern Territory, Australia	Fyler and Caira (2010)	15
A. icelandicum Manger, 1972	NR	NR	Dipturus batis	ENA	Faxa Bay, Western coasts Iceland	Manger (1972)	38
A. ijimai Yoshida, 1917	NR	MPM 22639	Hemitrygon akajei	WNP	Tokyo, Japan	Yoshida (1917), Williams (1969), Yang et al. (2016)	48
A. ijimai†	NR	NR	Hemitrygon akajei	WNP	East China Sea, Japan	Yamaguti (1952)	I
A. inbiorium Marques, Centritto & Stewart, 1997	CNHE 3137	USNPC 87373; CHIOC 33753a, b; CNHE 3138	Narcine entemedor	ECP	Cuajiniquil Beach, Gulf of Santa Helena, Guanacaste, Costa Rica	Marques et al. (1997b)	5‡
A. incognita (MacCallum, 1921) Wardle & McLeod, 1952	NR	NR	Dasyatis pastinaca	ENA, MED, ECA	New York Aquarium	MacCallum (1921), Southwell (1925), Williams (1969)	.
A. indicum (Subhapradha, 1955)	NR	NR	Narcine brasiliensis**	WSA	Madras Coast, India	Subhapradha (1955), Williams (1969)	58
A. intermedium Perrenoud, 1931	NR	NR	Dasyatis pastinaca**	ENA, MED, ECA	Tauranga, New Zealand	Perrenoud (1931)	48
A. jalalii Maleki, Malek & Palm, 2013	ZUTC 1291	ZUTC 1292–1295), SEM voucher ZUTC 1296); IPCAS C–639); ZMB E.7559	Pastinachus cf. sephen**	NIO	Gulf of Oman, Iran	Maleki et al. (2013)	15
A. jamesi Maleki, Malek & Palm, 2015	ZUTC 1328	ZMB E.7570; SEM voucher ZUTC 1329.	Rhynchobatus cf. djiddensis**	WIO, NIO	Persian Gulf, Iran	Maleki et al. (2015)	19
A. janineae Maleki, Malek & Palm, 2015	ZUTC 1311	ZUTC 1312–1316; ZMB E.7566; SEM vouchers ZUTC 1317–1318	Rhynchobatus cf. djiddensis**	WIO, NIO	Gulf of Oman, Iran	Maleki et al. (2015)	15

PO	15	\$9	48	51	1	2§	48	18	19
Sou	Fyler and Caira (2010)	Campbell and Beveridge (2002)	Bilqees (1980)	Maleki et al. (2019)	Reyda and Caira (2006)	Campbell and Beveridge (2002)	Yamaguti (1952), Yang et al. (2016)	Campbell and Beveridge (2002)	Vardo-Zalik and Campbell (2011)
Loc	Gove Harbor, Gulf of Carpentaria, Northern Territory, Australia	Cape Ford, North Australia	Karachi Coast, Pakistan	Chabahar coast, Gulf of Oman, Iran	Off Kampung Tetabuan, Sabah, Malaysia	Broome, Western Australia	Sea of Ariake, Kyusyu, Japan	Nickol Bay, Western Australia	Gulf of Mexico
PS	NIO, WNP	۸.	NIO, WCP, WNP	NIO, EIO, WCP, WNP	NIO, WCP	WIO, NIO	WNP	OIN	WCA, WNA
Species of Host	Rhynchobatus laevis**	Dasyatis sp.**	Mustelus manazo Bleeker, 1855	Gymnura cf. poecilura**	Pateobatis uarnacoides	Rhynchobatus djiddensis**	Hemitrygon akajei	Pastinachus sephen	Pseudobatos lentiginosus (Garman, 1880)
Nt, Pt or Va	QM G232503– G232505; USNPC 104279; LRP 7573–7575, cross sections of one paratype worm and voucher LRP 7580–7582, SEM LRP 7576–7578, hologenophore LRP 7579	SAM AHC 28228	SPUK 2000 (syntype)	ZCUOK 123–127; ZUTC Platy. 1336–1340, 1 SEM voucher ZUTC Platy. 1341	USNPC 97467– 97468; LRP 3860– 3865 (including cross sections and SEM specimens); MZUM (P) 177(p)–180(p); IPMB 77.08.16	SAM AHC 28248	NR	SAM AHC 28216	USNPC 103816– 103819
Ht	QM G232502	SAM AHC 28227	NR	ZCUOK 122	MZUM (P) 176(h)	SAM AHC 28247	MPM 22637	SAM AHC 28215	USNPC 103815
Species of Acanthobothrium	A. jeanneae Fyler & Caira, 2010	A. jonesi Campbell & Beveridge, 2002	A. karachiense Bilqees, 1980	A. kurdistanense Maleki, Malek & Palm, 2019	A. larsoni Reyda & Caira, 2006	A. lasti Campbell & Beveridge, 2002	A. latum Yamaguti, 1952	A. laurenbrownae Campbell & Beveridge, 2002	A. lentiginosum Vardo-Zalik & Campbell, 2011

РО	5) 15) 2\$	++) 1(8,9,5)‡	 	(2)	5 2	89), 4§	I	ı	6(3)‡
Sou	Reyda and Caira (2006)	Baer and Euzet (1962)	Campbell (1969)	Goldstein et al. (1969)	Goldstein et al. (1969)	Maheswari et al. (1985)	Severino and Verano (1980)	Southwell (1925)	Wang and Yang (2001), Yang et al. (2016)	Yang et al. (2016)	Yang et al. (2016)	Riser (1955)
Loc	Off Kampung Tetabuan, Sabah, Malaysia	Ceylon Pearl Bank, Sri Lanka	Chesapeake Bay, Virginia, USA	Gulf of Mexico, Texas, USA	Gulf of Mexico, Florida, USA	Waltair coast, India	Callao, Lima, Peru	Madras Coast, India	Xiamen, Fujiari, China	Off Guanghai Port, Guangdong, China	Sanya Fishing Port, Sanya, Hainan, China	Monterey Bay, California, USA
PS	NIO, WCP	۸.	WSA, WCA, WNA	WSA	WSA	WIO, NIO, EIO, WCP	ECP, ESP	۸.	WNP	WNP	WNP	ENP, ECP
Species of Host	Pateobatis uarnacoides	Dasyatis sp.**	Hypanus americanus	Narcine brasiliensis**	Narcine brasiliensis**	Himantura uarnak	Sympterygia brevicaudata (Cope, 1877)	Urogymnus sp.**	Hemitrygon akajei	Hemitrygon akajei	Hemitrygon akajei	Myliobatis californicus
Nt, Pt or Va	USNPC 97469; LRP 3866–3868 (including cross sections and SEM specimens); MZUM (P) 182(p)–183(p); IPMB 77.08.17	NR	USNPC 71354	USNPC 62939	USNPC 74851	NR	CH-MHNJP 343, 343a	NR	NR	MPM 21232; SYSU 20140620-1-7	NR	NR
Ht	MZUM (P) 181(h)	NR	USNPC 71353	USNPC 62938	NR	NR	CH-MHNJP 342	NR	MPM 21231	MPM 21231	NR	USNPC 37417
Species of Acanthobothrium	A. lepidum Reyda & Caira, 2006	A. lilium Baer & Euzet, 1962	A. lineatum Campbell, 1969	A. lintoni Goldstein, Henson & Schlicht, 1968	A. lintoni†	A. longipedunculata Meheswari, Sanaka, Lakshmi & Rao, 1985	A. lusarmientoi Severino & Verano, 1980	A. macracanthum Southwell, 1925	A. macrocephalum Wang & Yang, 2001	A. macrocephalum‡	A. macrocephalum†	A. maculatum Riser, 1955

Species of Acanthobothrium	Ht	Nt, Pt or Va	Species of Host	PЭ	Loc	Sou	Cd
A. magnum Euzet, 1959	NR	NR	Pteroplatytrygon violacea	ENP, ECP, ESP, WSA, WCA, WNA, ENA, MED, ECA, ESA, WIO, NIO, EIO, WSP, WCP, WNP	Mediterranean Sea, France	Euzet (1959)	48
A. makranense Maleki, Malek & Palm, 2019	ZCUOK 130	ZCUOK 131–135; ZUTC Platy. 1345–1350, 1 SEM voucher ZCUOK 139, 1 SEM voucher ZUTC Platy. 1350	Cymnura cf. poecilura**	NIO, EIO, WCP, WNP	Chabahar coast, Gulf of Oman, Iran	Maleki et al. (2019)	15
A. manteri Hassan, 1983	IHAHE S1051/A	IHAHE S1051/B	Pastinachus sephen**	NIO	Mediterranean Sea, Egypt	Hassan (1983)	58
A. margieae Fyler, 2011	NMNS 6356–001	NMNS 6356–002, 6356–003, 6356–004, 6356– 005, 6356–006, 6356–007; LRP 7468–7477; USNPC 103274	Orectolobus japonicus Regan, 1906	WNP, WCP	Off Penghu Island, East China Sea, Magong, Taiwan	Fyler (2011)	8€
A. marplatensis Ivanov & Campbell, 1998	MLP 4025	MLP 4026; USNMPC 87475; NHMUK 1998.2.10.1-2	Atlantoraja castelnaui (Miranda Ribeiro, 1907)	WSA	Mar del Plata, Buenos Aires, Argentina	Ivanov and Campbell (1998)	11
A. marquesi Rodríguez-Ibarra, Pulido-Flores, Violante-González & Monks, 2018	CNHE 10554	CNHE 10555, 10556; HWML 139377–139384; CHE P00061– P00063	Aetobatus cf. narinari**	WSA, WCA, WNA, ECA	Laguna de Términos, Ciudad del Carmen, Campeche, Mexico	Rodríguez-Ibarra et al. (2018)	€
A. marquesi†	NR	NR	Aetobatus cf. narinari**	WSA, WCA, WNA, ECA	Champotón, Campeche, Mexico	Rodríguez-Ibarra et al. (2018)	I
A. martini Campbell & Beveridge, 2002	SAM AHC 28213	SAM AHC 28214	Myliobatis tenuicaudatus Hector, 1877	EIO, WSP	Bunbury, Western Australia	Campbell and Beveridge (2002)	18

Species of Acanthobothrium	Ht	Nt, Pt or Va	Species of Host	PS	Loc	Sou	Cq
A. maryanskii Caira & Burge, 2001	CNHE 4171	CNHE 4172; LRP 2012, 2013; USNPC 90840, 90841	Diplobatis ommata	ECP	Loreto, Gulfo of California, Mexico	Caira and Burge (2001)	59
A. marymichaelorum Twohig, Caira & Fyler, 2008	(P) (MZUM(P) (P) (P) (P) (P) (P) (P) (P) (P) (P)	MZUM(P) 700(P)–702(P); SBC P–00028; USNPC 100700; LRP 4162– 4164 (whole mount), 4167–4168 (cross sections)	Brevitrygon walga (Müller & Henle, 1841)	OIN	Off Sematan, Sarawak, Malaysia	Twohig et al. (2008)	15
A. marymichaelorum	NR	NR	Brevitrygon walga	OIN	Off Mukah, Sarawak, Malaysia.	Twohig et al. (2008)	ı
A. masnihae Fyler & Caira, 2006	MZUM (P) 147	USNPC 96416– 96417; LRP 3825- 3835 (including cross sections and SEM specimens); MZUM (P) 148; IPMB 77.14.06	Urogymnus polylepis	NIO, WCP	Kampung Abai, Kinabatangan River, Sabah, Malaysia	Fyler and Caira (2006)	28
A. mathiasi Euzet, 1959	NR	N.	Mustelus mustelus	ENA, MED, ECA, ESA	Sète, France	Euzet (1959)	1§
A. mathiasi*	NR	NR	Mustelus canis (Mitchill, 1815)	WNA, WCA, WSA	Sète, France	Euzet (1959)	ı
A. matttaylori Fyler & Caira, 2010	QM G232508	Hologenophore USNPC 104281	Rhynchobatus laevis**	NIO, WNP	Gove Harbor, Gulf of Carpentaria, Northern Territory, Australia	Fyler and Caira (2010)	49
A. micracantha Yamaguti, 1952	NR	MPM 22635, 22636	Hemitrygon akajei	WNP	Nagasaki, East China Sea, Japan	Yamaguti (1952), Yang et al. (2016)	48
A. micracantha*	NR	NR	Gymnura micrura**	WSA, WCA, WNA, ECA	Nagasaki, East China Sea, Japan	Yamaguti (1952)	ı
A. micracantha*	NR	NR	Telatrygon zugei	WCP, WNP	Nagasaki, East China Sea, Japan	Yamaguti (1952)	1
A. microcephalum Alexander, 1953	USNPC 47852	NR	Myliobatis californicus	ENP, ECP	Long Beach Harbor, California, USA	Alexander (1953)	4‡

Species of Acanthobothrium	Ht	Nt, Pt or Va	Species of Host	PS	Loc	Sou	Cd
A. minus Tazerouti, Kechemir-	MNHN HEL 76,	MNHN HEL 77,	Raja asterias Delaroche,	ENA, MED	Cap Djinet, Algérie	Tazerouti et al. (2009)	29
Issad & Euzet, 2009	Th 180	Th 181, HEL 78,	1809				
		Th 182, HEL 79,					
		Th 183; NHMUK					
		2009.2.10.1-2					
A. minus†	NR	NR	Raja asterias	ENA, MED	Zemmouri El Bahri,	Tazerouti et al. (2009)	ı
					Algérie		
A. minus†	NR	NR	Raja asterias	ENA, MED	Bouharoun, Algérie	Tazerouti et al. (2009)	1
A. minusculus Marques, Brooks &	MEPN 3030	MNHG 22099;	Urobatis tumbesensis	ECP	Puerto Hualtaco,	Marques et al. (1997a)	1+
Barriga, 1997		HWML 39178,	(Chirichigno F. &		Provincia de El Oro,		
		CNHE 3030	McEachran, 1979)		Ecuador		
A. monksi Marques, Brooks &	MEPN 3031	MNHG 22100;	Aetobatus narinari**	WSA, WCA,	Puerto Jelí,	Marques et al. (1997a)	1
Barriga, 1997		HWML 39179;		WNA, ECA	Provincia de El Oro,		
		CNHE 3031			Ecuador		
A. mooreae Campbell & Beveridge,	SAM AHC 28209	SAM AHC 22665,	Trygonorrhina fasciata	WSP	Northhaven, South	Campbell and Beveridge	28
2002		22718, 28265			Australia	(2002)	
A. mujibi Bilqees, 1980	NR	SPUK 2001	Mustelus manazo	NIO, WCP,	Karachi Coast,	Bilgees (1980)	5 .
		(syntype)		WNP	Pakistan		
A. musculosum (Baer, 1948)	NR	NR	Pteroplatytrygon violacea	ENP, ECP,	New Zealand	Baer (1948), Euzet	48
Yamaguti, 1959				ESP, WSA,		(1959), Yamaguti	
				WCA, WNA,		(1959a), Williams (1969)	
				ENA, MED,			
				ECA, ESA,			
				WIO, NIO,			
				EIO, WSP,			
				WCP, WNP			
A. myliomaculata Srivastav, Shweta	DZCl	NR	Aetomylaeus maculatus	CP,	Madras Coast, India	Srivastav et al. (1995)	48
& Noopur, 1995			(Gray, 1834)	WNP			

Species of Acanthobothrium	Ht	Nt, Pt or Va	Species of Host	PS	Loc	Sou	СД
A. nanogravidum Zschoche, Caira & Fyler, 2011	QM G232166	QM G232167– G23217, cross sections QM G232171, G23217; USNPC 104103); LRP 7480–7483, cross sections LRP 7486–7491, SEM LRP 7484–7485), egg mounts LRP 7492–7493	Pastinachus ater (Macleay, 1883)	WIO, NIO, EIO, WSP, WCP	Gulf of Carpentaria off Weipa, Queensland, Australia.	Zschoche et al. (2011)	
A. nicoyaense Brooks & McCorquodale, 1995	USNPC 84477	USNPC 84388; MNHG 18255	Aetobatus narınari**	WSA, WCA, WNA, ECA	Punta Morales, Golfo de Nicoya, Costa Rica	Brooks and McCorquodale (1995)	! ! -
A. ningdense Yang, Sun, Zhi, Iwaki, Reyda & Yang, 2016	MPM 21226	MPM 21227, 21228; SYSU 20121113-1-3, 20141002-1-27	Hemitrygon akajei	WNP	Fuhai aquatic market, Ningde, Fujian Province, China	Yang et al. (2016)	4
A. ningdense†	X X	NR	Hemitrygon akajei	WNP	Off Wanjichi aquatic wholesale market, Taizhou, Zhejiang Province, China	Yang et al. (2016)	I
A. ningdense†	NR	NR	Hemitrygon akajei	WNP	8 th Seafood Market, Xiamen, Fujian Province, China	Yang et al. (2016)	ı
A. ningdense†	XX	NR	Hemitrygon akajei	WNP	Guanghai Port, Taishan, Guangdong Province, China	Yang et al. (2016)	1
A. ningdense†	NR	NR	Hemitrygon akajei	WNP	Sanya Fishing Port, Sanya, Hainan Province, China	Yang et al. (2016)	ı
A. obuncus Marques, Brooks & Barriga, 1997	MEPN 3032	MNHG 22101; HWML 39180; CNHE 3032, 3167	Hypanus longus	ECP	Puerto Hualtaco, Provincia de El Oro, Ecuador	Marques et al. (1997a)	‡9

Nt, Pt or Va	ies	Species of Host	P5	Loc	Sou	Cd
	SAM AHC 28202 SAM AHC 28203 Aptychotic $ $ (H ₃	Aptychotrema vincentiana (Haacke, 1885	EIO	Musgrave Shoal, South Australia	Campbell and Beveridge (2002)	28
313	QM 231345 QM G231346- U G231347; USNPC acantho 101957-101958; White LRP 4317-4318; cross sections QM 231349, QM G231348; SEM LRP 4319-4320, 4327-4328, hologenophores LRP 4321, LRP 4322	Urogymnus acanthobothrium Last, White & Kyne, 2016	WSP, WCP	Arafura Sea, east of Wessel Islands, Northern Territory, Australia.	Fyler et al. (2009), Caira and Jensen (2017)	1
SAM AHC 22699	SAM AHC 22699	Urolophus expansus	EIO	Holdfast Bay, South Australia	Campbell and Beveridge (2002)	1§
NR	NR <i>Urol</i> l Mc	Urolophus lobatus McKay, 1966	EIO	Esperance, Western Australia	Campbell and Beveridge (2002)	1
USNPC 71216	NR	Pseudobatos productus (Ayres, 1854)	ENP, ECP	Newport Beach, California, USA	Dailey and Mudry (1968)	2‡
NR	NR Pseudo (Gar	Pseudobatos planiceps (Garman, 1880)	ECP, ESP	Lima, Chorrillos, Peru	Iannacone et al. (2011)	I
NR	NR Urobatis	Urobatis halleri (Cooper, 1863)	ENP, ECP	Anaheim Bay, California, USA	Appy and Dailey (1973)	I
NR		Urobatis halleri	ENP, ECP	Puerto Peńasco, Sonora, Mexico	Friggens and Brown (2005)	I
ZCUOK 117	ZCUOK 118–122; <i>Gymnun</i> ZUTC Platy. 1330–1334, 1 SEM voucher ZUTC Platy. 1335	Gymnura cf. poecilura**	NIO, EIO, WCP, WNP	Chabahar coast, Gulf of Oman, Iran	Maleki et al. (2019)	19
NR	NR Gymnu	Gymnura cf. poecilura	NIO, EIO, WCP, WNP	Bandar Abbas, Persian Gulf, Iran	Maleki et al. (2019)	I
USNPC 49095	Z Z Z	Urobatis halleri	ENP, ECP	San Diego Bays,	Young (1954)	*:

Species of Acanthobothrium	Ht	Nt, Pt or Va	Species of Host	PS	Loc	Sou	Cd
A. parviuncinatum*	NR	NR	Gymnura marmorata (Cooper, 1864)	ECP	San Diego Bays, California, USA	Young (1954)	I
A. parviuncinatum†	NR	NR	Urobatis halleri	ENP, ECP	Puerto Peńasco, Sonora, Mexico	Friggens and Brown (2005)	I
A. parvum Manger, 1972	NR	NR	Dipturus batis	ENA	Faxa Bay, Western coasts Iceland	Manger (1972)	\$9
A. paulum Linton, 1890	NR	USNPC 07683, 35882, 71351, 71352.	Bathytoshia centroura	WSA, WCA, WNA	Woods Hole, Massachusetts, USA	Linton (1890), Vardo- Zalik and Campbell (2011)	1(8,9,5)‡
A. paulum*†	NR	NR	Raja eglanteria	WCA, WNA	Chesapeake Bay, Virginia, USA	Campbell (1969)	ı
A. paulum*†	NR	NR	Hypanus americanus	WSA, WCA, WNA	Chesapeake Bay, Virginia, USA	Campbell (1969)	I
A. pearsoni Williams, 1962	NR	NR	Orectolobus maculatus (Bonnaterre, 1788)	EIO, WSP	Hastings Point NSW, Australia	Williams (1962), Campbell and Beveridge (2002)	1\$
A. persicum Maleki, Malek & Palm, 2019	ZCUOK 135	ZCUOK 136–137; ZUTC Platy. 1351–1352, 1 SEM voucher ZCUOK 142, 1 SEM voucher ZUTC Platy. 1353	Gymnura cf. poecilura**	NIO, EIO, WCP, WNP	Bandar Abbas, Persian Gulf, Iran	Maleki et al. (2019)	19
A. peruviense Reyda, 2008	USNPC 99945	USNPC 99946; LRP 4108–4111 (including whole mounts and SEM specimens); MZUSP 6393a–6393b; MHNP 2335	Potamotrygon motoro (Müller & Henle, 1841)	WSA, WCA	Madre de Dios River at Boca Manu, Madre de Dios Department, Peru	Reyda (2008)	1(8)€
A. pichelinae Campbell & Beveridge, 2002	SAM AHC 28229	SAM AHC 28230	Myliobatis tenuicaudatus	EIO, WSP	Devonport, Tasmania	Campbell and Beveridge (2002)	48
A. pichelinae†	NR	NR	Myliobatis tenuicaudatus	EIO, WSP	Bunbury, Western Australia	Campbell and Beveridge (2002)	I

Species of Acanthobothrium	Ht	Nt, Pt or Va	Species of Host	PS	Loc	Sou	Cd
A. pintanensis Wang, 1984	NR	NR	Neotrygon kuhlit**	WSP	Fujian Province, China	Wang (1984)	49
A. polytesticularis Wang & Yang, 2001	PRLXU	NR	Squalus sp.**	۸.	Xiamen, Fujiari, China	Wang and Yang (2001)	48
A. ponticum Léon-Borcea, 1934	NR	NR	Raja clavata	ENA, MED, ECA, ESA, WIO	Agigéa, Black Sea	Léon-Borcéa (1934)	د.
A. ponticum*	NR	NR	Dasyatis pastinaca	ENA, MED, ECA	Agigéa, Black Sea	Léon-Borcéa (1935)	1
A. popi Fyler, Caira & Jensen, 2009	QM G231350	QM G231351- G231352; USNPC 101959-101960; LRP 4323-4324; cross sections QM G231353; SEM LRP 4329-4330, 4325-4326, hologenophores LRP 4331, 4332	Urogymnus acanthobothrium	WSP, WCP	Arafura Sea, east of Wessel Islands, Northern Territory, Australia.	Fyler et al. (2009), Caira and Jensen (2017)	25
A. ppdeleoni Zaragoza-Tapia, Pulido-Flores & Monks, 2020	CNHE 11253	CNHE 11254; HWML 216260	Hypanus dipterurus	ECP	Bahía de Chamela, Jalisco, Mexico	Zaragoza-Tapia et al. (2020)	25
A. psammobati Carvajal & Goldstein, 1969	USNPC 71357	USNPC 71358	Psammobatis scobina (Philippi, 1857)	ESP	South Pacific Ocean, between Papudo and Talcahuano, Chile	Carvajal-G. and Goldstein (1969)	5#
A. psammobati*†	NR	CH-MHNJP 342a, 342b	Sympterygia brevicaudata	ECP, ESP	Callao, Lima, Peru	Tantaleán-Vidaurre (1991)	ı
A. puertecitense Caira & Zahner, 2001	CNHE 4175	CNHE 4176; USNPC 90843; LRP 2105–2106	Heterodontus francisci	ECP, ESP	Puertecitos, Gulf of California, Mexico	Caira and Zahner (2001)	49
A. puntarenasense Marques, Brooks & Monks, 1995	MNHG 20005	MNHG 20006– 20007; HWML 38543, CNHE 4176.	Hypanus longus	ECP	Punta Morales, Puntarenas Province, Costa Rica	Marques et al. (1995)	2‡
A. quadripartitum Williams, 1968	NR	NR	Leucoraja naevus (Müller & Henle, 1841)	ENA, MED, ECA	North Sea, off Aberdeen	Williams (1968)	2§

Species of Acanthobothrium	Ht	Nt, Pt or Va	Species of Host	PS	Loc	Sou	Cd
A. quinonesi Mayes, Brooks & Thorson, 1978	USNPC 74804	USNPC 74805; HWML 74806	Potamotrygon magdalenae (Duméril, 1865)	WCA	Magdalena River, Cienaga Jobo, vicinity of San Cristobal, Bolivar, Colombia	Mayes et al. (1978)	7+
A. quinonest*†	NR	NR	Potamotrygon yepezi Castex & Castello, 1970	WCA	Lake Maracaibo area near El Congo and Represa de Tule, Rio Cachiri, Zulia, Venezuela	Brooks et al. (1981)	I
A. rajaebatis (Rudolphi, 1810) Euzet, 1959	NR	NR	Dipturus batis**	ENA	Mediterranean Sea	Rudolphi (1810)	58
A. rajaebatis*†	NR	NR	Dipturus oxyrinchus (Linnaeus, 1758)	ENA, MED, ECA	Sète, France	Euzet (1959)	I
A. rajaebatis*†	NR	NR	Rostroraja alba (Lacepède, 1803)	ENA, MED, ECA, ESA, WIO	Sète, France	Euzet (1959)	I
A. rajaebatis*†	NR	NR	Rostroraja alba	ENA, MED, ECA, ESA, WIO	Lacépède, France	Euzet (1959)	I
A. rajaebatis†	NR	NR	Dipturus batis**	ENA	Sète, France	Euzet (1959)	ı
A. rajaebatis†	NR	NR	Dipturus batis**	ENA	Roscoff, France	Euzet (1959)	ı
A. rajivi Ghoshroy & Caira, 2001	CNHE 4038	CNHE 4039; HWML 15552; LRP 2055–2056; USNPC 90461	Hypanus dipterurus	ECP	Puertecitos, Gulf of California, Mexico	Ghoshroy and Caira (2001)	2‡
A. ramiroi Ivanov, 2005	MACN-Pa 412/1- 4	USNPC 92521	Potamotrygon motoro	WSA, WCA	Río Colastiné, Santa Fé, Argentina	Ivanov (2005)	49
A. ramiroi†	NR	NR	Potamotrygon motoro	WSA, WCA	Río Coronda, Santa Fé, Argentina	Ivanov (2005)	I
A. regoi Brooks, Mayes & Thorson, 1981	USNPC 75709	USNPC 75710; HWML 21012, 21013	Potamotrygon hystrix (Müller & Henle, 1841)	WSA	Orinoco River Delta, Orinoco River near Los Castillos, Venezuela	Brooks et al. (1981)	5#

Species of Acanthobothrium	Ht	Nt, Pt or Va	Species of Host	PS	Loc	Sou	Cd
	N.R.	N. R.	Potamotrygon falkneri Castex & Maciel, 1963	WSA	Paraná River, Brazil	Lacerda et al. (2008)	I
	NR	NR	Potamotrygon motoro	WSA, WCA	Paraná River, Brazil	Lacerda et al. (2008)	ı
A. rhinobati Alexander, 1953	USNPC 47858	USNPC 47859	Pseudobatos productus	ENP, ECP	Santa Monica Harbor, California, USA	Alexander (1953)	9(5)‡
	NR	NR	Pseudobatos productus	ENP, ECP	Ocean Park Pier, California, USA	Alexander (1953)	I
A. robertsoni Campbell & Beveridge, 2002	SAM AHC 28197	SAM AHC 22590, 22591, 22592, 22667, 22714	Trygonorrhina fasciata	WSP	Middleton, South Australia	Campbell and Beveridge (2002)	38
	NR	SAM AHC 28257	Pristiophorus cirratus	EIO, WSP	Port Stanvac, South Australia	Campbell and Beveridge (2002)	I
	NR	NR	Aptychotrema vincentiana	EIO	North Haven, South Australia	Campbell and Beveridge (2002)	I
	NR	NR	Aptychotrema vincentiana	EIO	Goolwa, South Australia	Campbell and Beveridge (2002)	I
	NR	NR	Dentiraja cerva (Whitley, 1939)	EIO, WSP	Port Stanvac, South Australia	Campbell and Beveridge (2002)	I
	NR	NR	Dentiraja cerva	EIO, WSP	Holdfast Bay, South Australia	Campbell and Beveridge (2002)	I
	NR	SAM AHC 28260	Urolophus bucculentus Macleay, 1884	EIO, WSP	Rapid Head, South Australia	Campbell and Beveridge (2002)	1
	NR	SAM AHC 22699	Urolophus expansus	EIO	Holdfast Bay, South Australia	Campbell and Beveridge (2002)	I
	NR	SAM AHC 28256	Urolophus lobatus	EIO	Esperance, Western Australia	Campbell and Beveridge (2002)	I
	NR	NR	Trygonorrhina fasciata	WSP	Outer Harbour, South Australia	Campbell and Beveridge (2002)	I
	NR	NR	Trygonorrhina fasciata	WSP	North Haven, South Australia	Campbell and Beveridge (2002)	I
	NR	NR	Trygonorrhina fasciata	WSP	Port Stanvac, South Australia	Campbell and Beveridge (2002)	ı
	NR	NR	Trygonorrhina fasciata	WSP	Goolwa, South Australia	Campbell and Beveridge (2002)	I

Species of Acanthobothrium	Ht	Nt, Pt or Va	Species of Host	PS	Loc	Sou	Cd
A. robertsoni†	NR	NR	Trygonorrhina fasciata	WSP	Port Vincent, South Australia	Campbell and Beveridge (2002)	I
A. robertsoni†	NR	NR	Trygonorrhina fasciata	WSP	Queenscliff, Victoria, Australia	Campbell and Beveridge (2002)	l
A. robustum Alexander, 1953	USNPC 47856	USNPC 47857	Pseudobatos productus	ENP, ECP	Long Beach Harbor, California, USA	Alexander (1953)	4‡
A. robustum*†	NR	NR	Pseudobatos planiceps	ECP, ESP	Trujillo, Peru	Escalante-A. (1986)	ı
A. rodmani Fyler, Caira & Jensen, 2009	QM G231354	QM G231355- G231357; USNPC 101961–101963; LRP 4333–4335; cross sections QM G231359 G231358); cross sections LRP 4564–4569, 4563), longitudinal sections 4560–4562, 4559, SEM LRP 4336–4339, hologenophores LRP 4340, 4341	Urogymnus acanthobothrium	WSP, WCP	Arafura Sea, east of Wessel Islands, Northern Territory, Australia.	Fyler et al. (2009), Caira and Jensen (2017)	§ 9
A. rohdei Campbell & Beveridge, 2002	SAM AHC 28233	SAM AHC 28234	Urolophus lobatus	EIO	Esperance, Western Australia	Campbell and Beveridge (2002)	18
A. romanowi Fyler, Caira & Jensen, 2009	QM G231360	QM G231361– 231363; USNPC 101964–101966; LRP 4342–4344; cross sections QM G231365, G231364); cross sections LRP 4351–4356, SEM LRP 4345–4348, hologenophores LRP 4350, 4349.	Urogymnus acanthobothrium	WSP, WCP	Arafura Sea, east of Wessel Islands, Northern Territory, Australia.	Fyler et al. (2009), Caira and Jensen (2017)	1
A. rotundum Subhapradha, 1955	NR	NR	Rhynchobatus djiddensis	WIO, NIO	Madras Coast, India	Subhapradha (1955)	49

Species of Acanthobothrium	Ht	Nt, Pt or Va	Species of Host	рS	Loc	Sou	Сд
A. sinaloaensis Zaragoza-Tapia, Pulido-Flores & Monks, 2020	CNHE 11257	CNHE 11258; HWML 216262	Hypanus longus	ECP	La Puntilla, Mazatlán, Sinaloa, Mexico	Zaragoza-Tapia et al. (2020)	25
A. soberoni Ghoshroy & Caira, 2001	CNHE 4040	CNHE 4041–4042; HWML 15548; LRP 2057–2059; USNPC 90462	Hypanus dipterurus	ECP	Puertecitos, Gulf of California, Mexico	Ghoshroy and Caira (2001)	‡ 5
A. soberoni†	NR	NR	Hypanus dipterurus	ECP	Bahía de Los Angeles, Gulf of California, Mexico	Ghoshroy and Caira (2001)	1
A. soniae Zaragoza-Tapia, Pulido- Flores, Violante-Gonzalez & Monks, 2019	CNHE 11136	CNHE 11137; HWML 139978; CHE P00081	Narcine entemedor	ECP	Bahía de Acapulco, Playa Las Hamacas, Guerrero, Mexico	Zaragoza-Tapia et al. (2019)	29
A. southwelli Subhapradha, 1955	NR	NR	Rhinobatos schlegelii** Müller & Henle, 1841	WNP	Madras Coast, India	Subhapradha (1955)	18
A. sphaera Maleki, Malek & Palm, 2013	ZUTC 1298	ZUTC 1299–1307), SEM vouchers ZUTC 1308–1309; IPCAS C–641; ZMB E7560	Pastinachus cf. sephen**	NIO	Persian Gulf, Iran	Maleki et al. (2013)	25
A. stefaniae Franzese & Ivanov, 2018	MACN-Pa 624	MACN-Pa 625/1–6, 626/1–3, 627/1, 628/1–2; IPCAS C-786; LRP 9403– 9410	Discopyge tschudii Heckel, 1846	ESP, WSA	Coastal waters off Mar Chiquita City, Buenos Aires Province	Franzese and Ivanov (2018)	15
A. stefaniae†	NR	NR	Discopyge tschudii	ESP, WSA	Coastal waters off Villa Gesell, Argentina	Franzese and Ivanov (2018)	1
A. stefaniae†	NR	NR	Discopyge tschudii	ESP, WSA	Off San Clemente del Tuyú, Argentina	Franzese and Ivanov (2018)	ı
A. stefaniae†	NR	NR	Discopyge tschudii	ESP, WSA	Off Camarones, Argentina	Franzese and Ivanov (2018)	I
A. stevensi Campbell & Beveridge, 2002	SAM AHC 28198	SAM AHC 28199	Irygonorrhina fasciata	WSP	Marion Bay, South Australia	Campbell and Beveridge (2002)	2\$

Species of Acanthobothrium	Ht	Nt, Pt or Va	Species of Host	РS	Loc	Sou	Cd
A. stevensi†	NR	NR	Trygonorrhina fasciata	WSP	Goolwa, South Australia	Campbell and Beveridge (2002)	ı
A. stevensi†	NR	NR	Trygonorrhina fasciata	WSP	Coorong, Australia	Campbell and Beveridge (2002)	ı
A. tasajerasi Brooks, 1977	USNPC 73961	USNPC 73962; HWML 20261	Styracura schmardae	WCA	Caribbean Sea, La Cienaga, Magdalena, Colombia	Brooks (1977)	2#
A. tasajerasi*†	NR	NR	Hypanus guttatus (Bloch & Schneider, 1801)	WSA, WCA	Lake Maracaibo, Venezuela	Mayes and Brooks (1981)	I
A. terezae Rego & Dias, 1976	CHIOC 31.215c	CHIO 10.847, 10.994, 31.412a-b, 31.215a-b	Potamotrygon motoro	WSA, WCA	Rio Salobra, Mato Grosso, Brazil	Rêgo and Luna Dias (1976)	4‡
A. tetabuanense Reyda & Caira, 2006	MZUM (P) 184(h)	USNPC 97470– 97471; LRP 3869– 3873 (including cross sections and SEM specimens); MZUM (P) 185(p)–186(p); IPMB 77.08.18	Pateobatis uarnacoides	NIO, WCP	Off Kampung Tetabuan, Sabah, Malaysia	Reyda and Caira (2006)	2€
A. thomasae Campbell & Beveridge, 2002	SAM AHC 28201	SAM AHC 22676	Aptychotrema vincentiana	EIO	Musgrave Shoal, South Australia	Campbell and Beveridge (2002)	2§
A. thomasae†	NR	NR	Aptychotrema vincentiana	EIO	Cowell, Australia	Campbell and Beveridge (2002)	ı
A. tortum (Linton, 1916) Baer & Euzet, 1962	NR	NR	Aetobatus narinari	WSA, WCA, WNA, ECA	Woods Hole, Massachusetts, USA	Linton (1916)	3‡
A. tortum†	NR	NR	Aetobatus narinari	WSA, WCA, WNA, ECA	Caimare Chico, Gulf of Venezuela	Mayes and Brooks (1981)	I
A. tortum†	NR	USNPC 70494	Aetobatus narinari	WSA, WCA, WNA, ECA	Cape Haze Marine Laboratory, Sarasota, Florida.	Campbell (1970)	I
A. triacis Yamaguti, 1952	NR	NR	Triakis scyllium Müller & Henle, 1839	WNP	Hamazima, Mie, Japan	Yamaguti (1952)	49
A. tripartitum Williams, 1969	NR	NR	Raja microocellata Montagu, 1818	ENA, ECA	English Channel, Plymouth	Williams (1969)	2§

Raja texana WCA Gulf of Mexico Myliobatis californicus ENP, ECP Long Beach Harbor, California, USA Urogymuus asperrimus ECA, WIO, Gulf of Mannar, IB01) MNP (Bloch & Schneider, 1841 NIO, EIO, Gulf of Mannar, India MNP Müller & Henle, 1841 WSP, WCP, Tasmania Adelaide, South Australia Urolophus paucimaculatus EIO, WSP Glenelg Beach near Adelaide, South Australia Urolophus paucimaculatus WCA Caragena, Colombia Schultz, 1949 WSA, WCA Lake Maracaibo, Venczuela Hypanus guttatus WSA, WCA Lake Maracaibo, Venczuela Hypanus longus ECP Puntarenas Province, Costa Rica Puntarenas Pastinachus sephen** NIO Province, Costa Rica Pastinachus sephen*** NIO Nickol Bay, Western Australia Himantura uarnak WIO, NIO, Waltair coast, India Eno, WCP Econaja nasuta (Müller & WSP Petone Beach, New Henle, 1841) Zeanaja Petone Beach, New	Species of Acanthobothrium	Ht	Nt, Pt or Va	Species of Host	PЭ	Loc	Sou	СД
USNPC 47855 NR Mylebatis californicus ENI; ECP Long Beach Harbor, California, USA	<i>ılmeri</i> Vardo-Zalik & npbell, 2011	USNPC 103830	USNPC 103831– 103837, 103839, 103842, 103846	Raja texana	WCA	Gulf of Mexico	Vardo-Zalik and Campbell (2011)	15
NR Urogymus aperrinus ECA, WIO, EO, Gulf of Mannar, IS01) Gelf of Mannar, India USNPC 72284 USNPC 72284 Trygonoptera testacea Miller & Henle, 1841 WSP Glenelg Beach near Adelaide, South Australia NR NR Urolaphus paucimaculatus EIO, WSP Glenelg Beach near Adelaide, South Australia USNPC 75162 USNPC 75163; Urobatis venezuelae WCA Glenelg Beach near Tasmania WCA Grategena, Schultz, 1949 NR NR Hypanus guttatus WSA, WCA Lake Maracaibo, Venezuela NR NR Hypanus guttatus WSA, WCA Lake Maracaibo, Venezuela NR Hypanus guttatus WSA, WCA Lake Maracaibo, Venezuela NR Hypanus guttatus WSA, WCA Lake Maracaibo, Venezuela NR Hypanus longus ECP Punta Morales, Venezuela ANHG 20013; HWML Hymatic entemedor ECP Punta Morales, Puntarcas, Puntatus, Saphen** 199981; CHE P00082 Pastinachus sephen*** P00082 P00082 Pastinacus, Mexico NR Himantura uamade WIO, NIO, Waltair coast, India NR Himantura uamade WIO, WSP NR Himantura uamade	unilateralis Alexander, 1953	USNPC 47855	NR	Myliobatis californicus	ENP, ECP	Long Beach Harbor, California, USA	Alexander (1953)	7(2)‡
USNPC 72284 USNPC 72284 Trygonoptera testacea WSP Glenelg Beach near Adelaide, South Australia NR NR Urolophus paucimaculatus EIO, WSP Devonport, Tasmania USNPC 75162 USNPC 75163; Urobatis venezuelae WCA Cartagena, Schultz, 1949 Colombia NR NR Hypanus guttatus WSA, WCA Lake Maracaibo, Venezuela NN Hypanus guttatus WSA, WCA Isla Margarita, Venezuela NNHG 20011 MNHG 20012— Hypanus guttatus WSA, WCA Isla Margarita, Venezuela NNH Hymanus Guttatus WSA, WCA Isla Margarita, Venezuela NNH Hymanus Guttatus WSA, WCA Isla Margarita, Venezuela NNH Hymanus Guttatus WSA, WCA Isla Margarita, Venezuela NNH Hypanus Guttatus Isla Margarita, Isl	trogymni (Hornell, 1912)	NR	NR	Urogymnus asperrimus (Bloch & Schneider, 1801)	ECA, WIO, NIO, EIO, WSP, WCP, WNP	Gulf of Mannar, India	Hornell (1912), Southwell (1925)	.
NR NR CASTOR Colombia Tasmania USNPC 75163; Usolatis venezuelae WCA Cartagena, HWML 20917 Schultz, 1949 Colombia NR Hypanus guttatus WSA, WCA Lake Maracaibo, NR Hypanus guttatus WSA, WCA Isla Margarita, NRHG 20013; HWML 20010; HWML 20013; HWML 20010; HWML 20013; HWML 20010; Himantura uarnak 20013; HWML 20010; Hypanus guttatus 20013; Hypanus 20013; HWML 20010; Hypanus 20013; HWML 20013; HWML 20010; Hypanus 20013; HWML 20010; Hypanus 20013; Hypanus 20013; HWML 20010; Hypanus 20013; HWML 20010; Hypanus 20013	<i>urolophi</i> Schmidt, 1973	USNPC 72284	USNPC 72284		WSP	Glenelg Beach near Adelaide, South Australia	Schmidt (1973)	18
USNPC 75162 USNPC 75163; Urobatis venezuelae WCA Cartagena, Colombia NR HWML 20917 Schultz, 1949 Lake Maracaibo, Venezuela NR Hypanus guttatus WSA, WCA Lake Maracaibo, Venezuela NR Hypanus longus ECP Puntra Morales, Venezuela MNHG 20011 MNHG 20012- Hypanus longus ECP Puntra Morales, Puntra L39979- Puntra macas, Puntra Hamacas, Puntra L39981; CHE Pastinachus sephen** NIO Nickol Bay, Western Australia NR NR Himantura uarnak WIO, NIO, Waltair coast, India EIO, WCP Petone Beach, New Henle, 1841)	ırolophi*†	NR	NR	Urolophus paucimaculatus	EIO, WSP	Devonport, Tasmania	Campbell and Beveridge (2002)	ı
NR Hypanus guttatus WSA, WCA Lake Maracaibo, Venezuela NR Hypanus guttatus WSA, WCA Isla Margaita, Venezuela MNHG 20011 MNHG 20012- Hypanus longus ECP Punta Morales, Puntarenas 38545 CNHE 11134 CNHE 11135; Narcine entemedor ECP Bahía de Acapulco, HWML 139981; CHE P00082 SAM AHC 28219 SAM AHC 28220 Pastinachus sephen** NIO Nickol Bay, Western Australia NR Himantura uarnak WIO, NIO, Waltair coast, India EIO, WCP Zeanaja nasuta (Müller & WSP Petone Beach, New Henle, 1841) Zealand	trotrygoni Brooks & Mayes,	USNPC 75162	USNPC 75163; HWML 20917	Urobatis venezuelae Schultz, 1949	WCA	Cartagena, Colombia	Brooks and Mayes (1980)	2‡
MNHG 20011 MNHG 20012- Hypanus guttatus WSA, WCA Isla Margarita, Venezuela 20013; HWML 38545 Province, Costa Rica 38545 Province, Costa Rica HWML 139979- Province, Costa Rica Punta In 139981; CHE HWML 139979- Province, Costa Rica Phymatical Province, Costa Rica Phymatical Province, Costa Rica Phymatical Province, Costa Rica Phymatical Phym	trotrygoni*†	NR	NR	Hypanus guttatus	WSA, WCA	Lake Maracaibo, Venezuela	Mayes and Brooks (1981)	ı
MNHG 20011 MNHG 20012– Hypanus longus ECP Punta Morales, 20013; HWML 38545 Narcine entemedor ECP Bahía de Acapulco, HWML 139979- 139981; CHE 139981; CHE Playa Las Hamacas, Guerrero, Mexico P00082 SAM AHC 28220 Pastinachus sephen** NIO Nickol Bay, Western Australia NR Himantura uarnak WIO, NIO, Naltair coast, India Humantura uarnak Helo, WSP Petone Beach, New Henle, 1841) Zealand	trotrygoni*†	NR	NR	Hypanus guttatus	WSA, WCA	Isla Margarita, Venezuela	Mayes and Brooks (1981)	ı
CNHE 11134 CNHE 11135; Narcine entemedor ECP Bahía de Acapulco, HWML 139979- HWML 139981; CHE P00082 SAM AHC 28219 SAM AHC 28220 Pastinachus sephen** NIO Nickol Bay, Western Australia NR Himantura uarnak WIO, NIO, Waltair coast, India EIO, WCP EIO, WCP Himantura (Müller & WSP Petone Beach, New Henle, 1841) SAM AHC 28219 SAM AHC 28220 Pastinachus sephen** NIO Nickol Bay, Western Australia Himantura uarnak WIO, NIO, Waltair coast, India EIO, WCP EIO, WCP EIO, WCP Australia	argasi Marques, Brooks & nks, 1995	MNHG 20011	MNHG 20012– 20013; HWML 38545	Hypanus longus	ECP	Punta Morales, Puntarenas Province, Costa Rica	Marques et al. (1995)	2++
SAM AHC 28219 SAM AHC 28220 Pastinachus sephen** NIO Nickol Bay, Western Australia NR Himantura uarnak WIO, NIO, Waltair coast, India NR DMNZ 194b,c,d, Zearaja nasuta (Müller & WSP Petone Beach, New 195–197 (syntype) Henle, 1841)	idali Zaragoza-Tapia, Pulido- es, Violante-Gonzalez & nks, 2019	CNHE 11134	CNHE 11135; HWML 139979- 139981; CHE P00082	Narcine entemedor	ECP	Bahía de Acapulco, Playa Las Hamacas, Guerrero, Mexico	Zaragoza-Tapia et al. (2019)	64
NR Himantura uarnak WIO, NIO, Waltair coast, India EIO, WCP EIO, WCP NR DMNZ 194b,c,d, Zearaja nasuta (Müller & WSP Petone Beach, New 195–197 (syntype) Henle, 1841) Zealand	valkeri Campbell & Beveridge,	SAM AHC 28219	SAM AHC 28220	Pastinachus sephen**	NIO	Nickol Bay, Western Australia	Campbell and Beveridge (2002)	2§
NR DMNZ 194b,c,d, Zearaja nasuta (Müller & WSP Petone Beach, New 195–197 (syntype) Henle, 1841) Zealand	valtairensis Uma Maheswari, aka, Vijaya Lakshmi & umantha Rao, 1987	NR	NR	Himantura uarnak	WIO, NIO, EIO, WCP	Waltair coast, India	Maheswari et al. (1987)	38
	vedli Robinson, 1959	NR	DMNZ 194b,c,d, 195–197 (syntype)	Zearaja nasuta (Müller & Henle, 1841)	WSP	Petone Beach, New Zealand	Robinson (1959)	48

Species of Acanthobothrium	Ht	Nt, Pt or Va	Species of Host	РS	Loc	Sou	Cd
A. wedli†	NR	NR	Zearaja nasuta	WSP	Portobello, Otago Harbour, New Zealand	Robinson (1959)	1
A. wedli†	NR	NR	Zearaja nasuta	WSP	South Island, off Lyttelton, New Zealand	Campbell and Beveridge (2002)	1
A. westi Vardo-Zalik & Campbell, 2011	USNPC 103841	USNPC 103838, 103840, 103843– 103845, 103847	Raja texana	WCA	Gulf of Mexico	Vardo-Zalik and Campbell (2011)	16
A. woodsholei Baer, 1948	NR	MNHG 40028 (syntype)	Bathytoshia centroura	WSA, WCA, WNA	Woods Hole, Massachusetts, USA	Baer (1948), Vardo-Zalik and Campbell (2011)	2(7)‡
A. woodsholei†	NR	NR	Bathytoshia centroura	WSA, WCA, WNA	Western North Atlantic	Goldstein (1964)	ı
A. xiamenensis Yang & Lin, 1994	NR	NR	Rhynchobatus djiddensis**	WIO, NIO	Xiamen, South Fujian, China	Yang (1994)	58
A. zainali Fyler & Caira, 2006	MZUM (P) 151	USNPC 96420– 96422; LRP 3844- 3849 (including cross sections and SEM specimens); MZUM (P) 152–153; IPMB 77.14.08	Urogymnus polylepis	NIO, WCP	Off Kampung Abai, Kinabatangan River, Sabah, Malaysia	Fyler and Caira (2006)	18
A. zapterycum Ostrowski de Nuńez, 1971	MACN-Pa 214/1	NR	Zapteryx brevirostris (Müller & Henle, 1841)	WSA	Mar del Plata, Buenos Aires, Argentina	Ostrowski de Núñez (1971)	2#
A. zapterycum†	NR	MACN-Pa 214/1- 2, 214/4–5, 629/1, 630/1–3, 631/1–4, 632/1–4; IPCAS C-787; LRP 9411– 9417	Zapteryx brevirostris	WSA	Coastal waters off Villa Gessel, Argentina	Franzese and Ivanov (2018)	I
A. zapterycum†	NR	NR	Zapteryx brevirostris	WSA	La Lucila del Mar, Argentina	Franzese and Ivanov (2018)	ı
A. zapterycum†	NR	NR	Zapteryx brevirostris	WSA	Puerto Quequén, Argentina	Franzese and Ivanov (2018)	ı

Species of Acanthobothrium	Ht	Nt, Pt or Va	Species of Host	PS	Loc	Sou	Cd
A. zapterycum†	NR	NR	Zapteryx brevirostris	WSA	Puerto Pirámides, Argentina	Franzese and Ivanov (2018)	J
A. zimmeri Fyler, Caira & Jensen, 2009	QM G231366	QM G231367– G231369; USNPC 101967–101969; LRP 4357–5358; cross sections QM G231371, G231370); cross sections LRP 4364–4366, SEM LRP 4359–4361, hologenophores LRP 4363, 4362	Urogymnus acanthobothrium	WSP, WCP	Arafura Sea, east of Wessel Islands, Northern Territory, Australia.	Fyler et al. (2009), Caira and Jensen (2017)	15
A. zschokkei Baer, 1948	MHNG 88/39	NR	Torpille (common name)**	۸.	Naples, Italy	Baer (1948)	\$9
A. zschokkei*†	NR	NR	Torpedo marmorata	ENA, MED, ECA, ESA	Adriatic Sea, Mediterranean Sea	Goldstein (1967)	I
A. zschokkei*†	NR	NR	Torpedo torpedo	ENA, MED, ECA	Sète, France	Euzet (1959)	1
A. zschokkei*†	NR	NR	Torpedo torpedo	ENA, MED, ECA	Adriatic Sea, Mediterranean Sea	Goldstein (1967)	ı

Results

The information obtained from the metadata analysis (Table 1) is comprised of 336 reports of the 201 valid species of *Acanthobothrium*. The list includes the type host of each species, type locality, and additional hosts and/or localities. Five of the elasmobranchs that were reported as hosts of *Acanthobothrium* were only identified to genus and four others are reported as "cf." (= similar to) (see Table 1).

The type localities where species of *Acanthobothrium* have been reported is shown in Figure 1. The currently known diversity of sharks comprises 517 species (34 families); of these, 19 species of sharks (eight families) have been reported to be parasitized by species of *Acanthobothrium* (Fig. 2). Eighteen of the 201 valid species have been described from sharks. The families of sharks that have the highest number of reports are Orectolobidae (three different species of *Acanthobothrium*), Heterodontidae (five species) and Triakidae (six species) (Fig. 2B). In contrast, currently known diversity of rays comprises 637 species (26 families); of these, 95 species (18 families) have been reported to be parasitized by species of *Acanthobothrium* (Fig. 3). Of the 201 valid species of *Acanthobothrium*, 182 have been described from rays. The families of rays that have the highest number of reports are Rajidae (20 species of *Acanthobothrium*) and Dasyatidae (70 species) (Fig. 3B).

Species of *Acanthobothrium* are not evenly grouped in the different categories. In Category 1 there are 55 species, 44 in Category 2, 19 in Category 3, 37 in Category 4, 17 in Category 5, 14 in Category 6, four in Category 7, four in Category 8, and three in Category 9. Although there is a Category 10, species in that category also are in grouped with those in Category 8 because their characteristics are thought to fall into both categories (Table 1). The categories of four species of *Acanthobothrium* were classified as unknown ("?") because the original descriptions do not have sufficient information for assignment in one of the ten categories (Table 1).

Discussion

Currently, 517 species of sharks have been described worldwide with 3.7% (19 of the 517 species) have been reported as hosts for species of *Acanthobothrium* (Fig. 2C). In contrast, 637 species of rays have been described with 14.9% (95 of the 637 species) have been reported as hosts for species of *Acanthobothrium* (Fig. 3C). Estimates of cestode diversity in elasmobranchs discussed by Caira (2011) assumes that the fauna of cestodes of a species of elasmobranchs does not vary substantially across in its distribution. Knowledge of life cycles are essential in understanding the distribution of species of *Acanthobothrium*; however, for this study it is assumed that the distribution of adults of these parasites normally is limited to that of its normal definitive host. Thus, it is hypothesized that the limits of the distribution of the host limits the species of its parasites to the same biogeographic regions proposed for the distribution of elasmobranchs by Last et al. (2016b). It is recognized that an infected elasmobranch

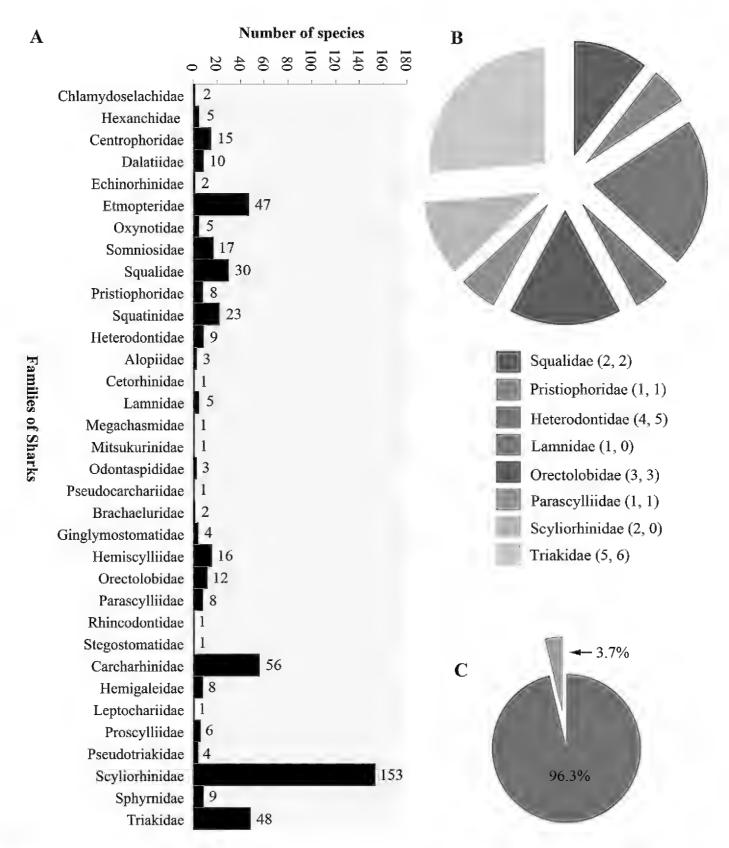


Figure 2. Families of sharks: **A** number of species of sharks per family **B** number of species of sharks parasitized by species of *Acanthobothrium*. Note: The first number within parentheses corresponds to the number of species of shark that have been reported as hosts of *Acanthobothrium* and the second is the number of species that have been described from that Family **C** percentage of species of shark reported to be parasitized within the total number of families of sharks- note: Red color = parasitized; Blue color = not parasitized.

could move outside of the region where it has been designated, but until an extension to its distribution has been reported, it must be assumed that the normal distribution for each species of parasite also is that same designated region. The information in the table will be subject to future research, not forgetting that there is a lack of knowledge of the life cycle of the species of *Acanthobothrium*; a partial life cycle of a single species

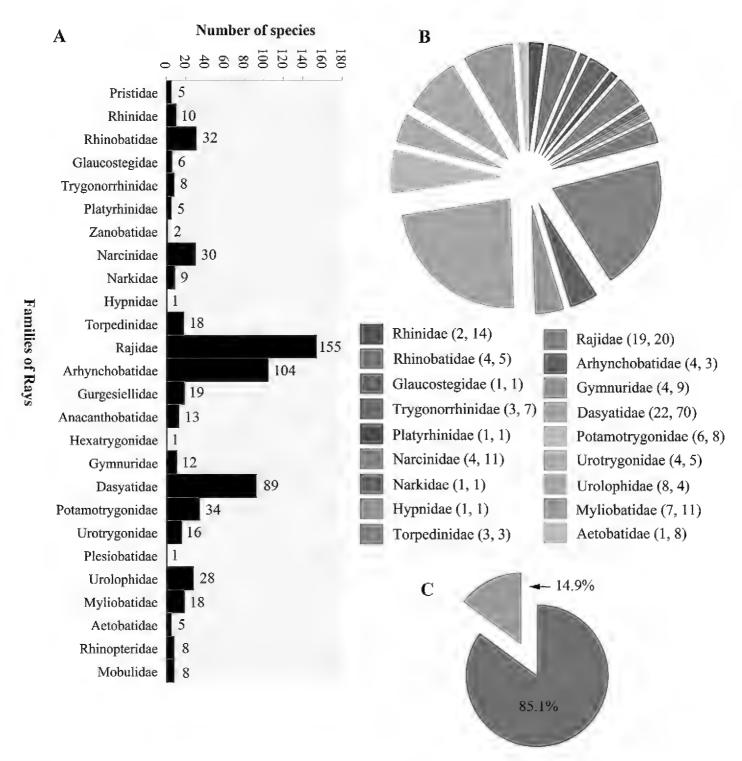


Figure 3. Families of rays: **A** number of species of rays per family **B** number of species of rays parasitized by species of *Acanthobothrium*. Note: The first number within parentheses corresponds to the number of species of ray that have been reported as hosts of *Acanthobothrium* and the second is the number of species that have been described from that Family **C** percentage of species of rays reported to be parasitized within the total number of families of rays- note: Red color = parasitized; Blue color = not parasitized.

has been reported (Holland and Wilson 2009). Publication of molecular sequences for more species will provide new discoveries in this subject.

The information in the Figures 1 and 4 indicates that there is an absence of reports from several regions of the world, such as ECA, ESA, WIO, ARC, and SOC. According to the percentages of species of elasmobranchs that have been reported as hosts of species of *Acanthobothrium*, we can infer that there are still many new species of *Acanthobothrium* to be discovered. In the GenBank database records, molecular sequences

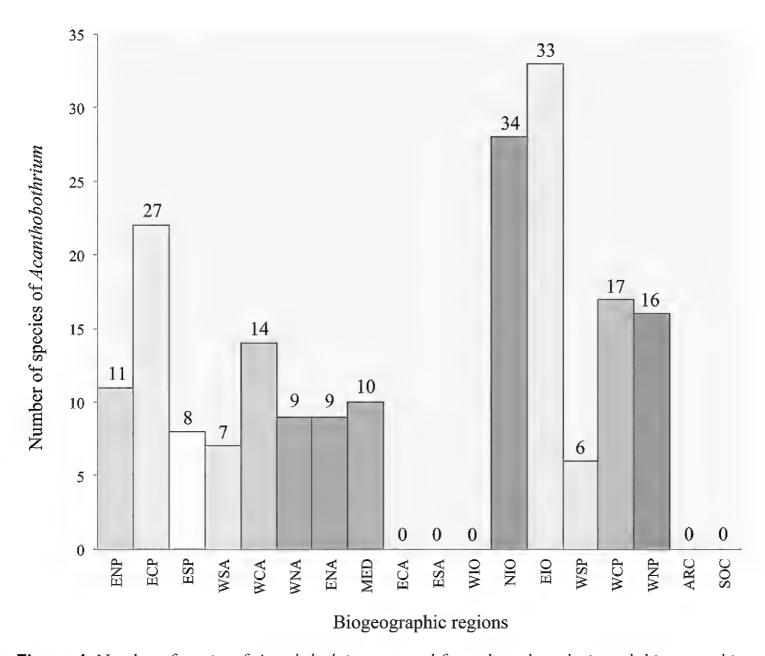


Figure 4. Number of species of *Acanthobothrium* reported from elasmobranchs in each biogeographic region (Last et al. 2016b).

of only 16 of the 201 species of *Acanthobothrium* have been reported. However, more molecular information about species of *Acanthobothrium* is required for future analyzes, both for identification and life cycle studies; these would provide more solid information for delimiting distributions.

In Table 1, *Acanthobothrium chilensis* Rêgo, Vicente & Herrera, 1968, was included for reference, although it was described from a fish, *Sarda chiliensis* (Cuvier, 1832) (Perciformes: Scombridae) (see Rêgo et al. 1968). Extensive recent studies of this species of fish (Chero et al. 2016; Luque et al. 2016) failed to report *A. chilensis*; there is only the report by Rêgo et al. (1968). The report of the host for this species of *Acanthobothrium* likely is an accidental infection and not a normal host.

According to Fyler et al. (2009) and Franzese and Ivanov (2018), species of *Acanthobothrium* appear to exhibit oioxenous specificity for their elasmobranch hosts. In the present metadata analysis, for species exclusively in elasmobranchs, 83% of the species of *Acanthobothrium* show remarkable host specificity for their definitive host, and thus, should be considered to be an oioxenous species. In contrast, 34 of the 200

species (17%) of *Acanthobothrium* have been reported in more than one species of elasmobranch (Table 1). However, with the metadata analysis of the distribution of the hosts and the reports of the species of *Acanthobothrium*, 45 of the type specimens of *Acanthobothrium* require confirmation of the host (Table 1) because some appear to be problematic identifications and other hosts were reported as "cf." or only as an unidentified member of a particular genus In addition, there are reports of species of *Acanthobothrium* that suggest misidentification of the parasites; these should reevaluated in future studies. To mention obvious cases, *A. batailloni* has been reported from the Mediterranean Sea and from the Pacific coast of Peru and Chile and *A. brevissime* has been reported from the Gulf of Mexico and the Pacific coast of Peru.

The categorical method developed by Ghoshroy and Caira (2001) was proposed in order to delimit the number of taxonomic comparisons when describing new species. Using the method of Ghoshroy and Caira (2001), which focused only on species from the Americas, Fyler and Caira (2006) later applied the same methodology to biodiversity data for species from other regions; those works are augmented by this study. Of the 201 known species of *Acanthobothrium*, 13 have been classified in more than one category (see category designations in Table 1) because some characteristics of those species overlap with those of more than one category (see descriptions found in Zschokke 1888; Linton 1890; Baer 1948; Alexander 1953; Euzet 1955; Riser 1955; Yamaguti 1959; Goldstein 1964; Williams 1969; Goldstein et al. 1969; Appy and Dailey 1973; Severino and Sarmiento 1979; Marques et al. 1997; Reyda 2008). This does not decrease the usefulness of the categorical method as a tool for the initial stages in identification.

Having more information, such as molecular sequences, could solve some problems in identification, such as the two cases mentioned above. A species of *Acanthobothrium* that has been assigned to more than one category suggests that the categories still need some refining, or it is an example of cryptic species that cannot be distinguished without molecular information. However, molecular information cannot replace morphological descriptions of species. One reason is the lack of material for sequencing of the vast majority of already-known species. Morphology also augments molecular data in studies of the phylogeny of platyhelminths (Zamparo et al. 2001; Littlewood 2008). A complete phylogenetic hypothesis based on total evidence (morphological and molecular data) such as that of Littlewood (2008) for any major group of cestodes is still distant. Until that time, a categorical method provides the easiest and most direct method for selection of a group of species similar to a new species of *Acanthobothrium*. This updated database includes the category designation for each species described to date will be an important tool for the future taxonomic studies.

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